Studies on the deep-sea Protobranchia (Bivalvia): the family Nuculidae

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CONTENTS

SYNOPSIS. The morphology, geographical distribution and adaptations to life in deep water of ten species of the family Nuculidae (Bivalvia: Protobranchia) from the Atlantic are described. These include four new species. The evolution of the family and the origins of the deep-water species are discussed and the taxonomy of the family reassessed.

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INTRODUCTION

This paper forms part of a continuing investigation of the biology of deep-sea protobranch bivalves of the Atlantic. (Allen & Hannah, 1989; Allen & Sanders, 1973, 1982; Sanders & Allen, 1973, 1977, 1985). The present study includes an appraisal of the biology, systematics and antiquity of ten species of the deep-sea Nuculidae.

From the time of Linneaus taxonomists have had difficulty in classifying the Nuculidae (eg. Hancock, 1846; Adams, 1856; Sowerby, 1871; Seguenza, 1877; Jeffreys, 1881; Verrill, 1884; Reeve, 1885; Dall, 1886; Hedley, 1902; Iredale, 1931, Schenck, 1934, 1939; Allen, 1954; James, 1972; Lubinsky, 1972). The nuculids were originally regarded as members of the family Arcidae. The type species of the genus *Nucula*, and of the family Nuculidae, is *Arca nucleus* Linné. This is now generally accepted as equivalent to *Nucula nucleus* auct. As with other protobranch groups (Allen, 1978) taxonomic difficulties arise because of the very great conservativeness of shell and body form.

The Subfamily *Nuculacea* has a long fossil record possibly dating from the Ordovician. The apparent stasigenesis involving few cladogenetic events possibly results from an early adaptation to a common homogeneous environment that has persisted throughout much of the zoic period. The magnitude of this early adaptation appears to have left little room for selective pressure change. For example, Levinton & Bambach, (1975) in a comparative study of Silurian and Recent deposit-feeding bivalve communities found that non-siphonate deposit-feeding nuculaceans were dominant forms in the non-compacted, watery sediments of both environments, even though separated by 400 million years. The Silurian counterpart to *Nucula* was a species of *Praenucula* which is similar in size and morphology to *Nucula* and probably had similar life style as an active deposit feeder, just below the sediment-water interface. Rhoads & Young, (1970) found that intensive near-surface reworking of the

sediment by non-siphonate protobranchs (*Nucula proxima*) creates an unstable, fluidized sediment. Similar conditions are thought to have been created by *Praenucula* in corresponding Silurian environments (Levinton & Bambach, 1975). According to Rhoads & Young, (1970) this has the effect of excluding siphonate forms and suspension feeders from the deposit-feeder biotope. The reduced competition resulting from the exclusion by non-siphonate protobranchs of more advanced forms, especially those of the massive post-Palaeozoic radiation of infaunal, siphonate heterodonts (Stanley, 1968), may further help to explain why the nuculoid forms have persisted virtually unchanged for such an enormous period of time. This ability to thrive in fluid sediments also pre-adapted the nuculids for a deep-sea existence.

The nuculids have been regarded as being close to the stem stock of many proposed phylogenies of the bivalves (eg. Pelseneer, 1911; Yonge, 1939) and, even though they are not now regarded as being similar to the ancestral bivalve (Atkins, 1938; McAlester, 1964; Allen & Sanders, 1969; Morris & Fortey, 1976; Babin, 1977; Allen, 1985), they are probably close to the ancestral stock of the subclass Protobranchia. An examination of the fossil record has been carried out to endeavour to establish which of the extant species are close to the ancestral stock furthermore, because the nuculids are such an archaic group it was thought that it might provide a contribution to the debate on the origin and antiquity of deep-sea fauna.

MATERIAL & METHODS

Specimens used in this study were sampled as follows: 1) Marine Biological Association of the United Kingdom (1967)—Bay of Biscay, R.V. 'Sarsia'; 2) Institute of oceanographic Science, U.K. (1968)—between Fuerteventura and the West African coast, RRs 'Discovery'; 3) Centre National de tri d'Oceanographic Biologique, France—Walda (1971), between Nigeria and the Angola, R.V. 'Jean Charcot'; Biogas (1972–74)—Bay of Biscay, R.V. 'Jean Charcot', R.V. 'La Perle' and R.V. 'Cryos'; Incal (1976), Rockall Trough and the North East Atlantic, R.V. 'Jean Charcot'; 4) Woods Hole Oceanographic Institute, U.S.A.—North America Basin (1961–73), Gayhead-Bermuda transect, R.V. 'Atlantis', R.V. 'Atlantis II', R.V. 'Chain', and R.V. 'Knorr'; Cape Verde Basin (1967), between Dakar and Recife, R.V. 'Atlantis II'; Angola Basin (1968), between Walvis Bay and Luanda, R.V. 'Atlantis II'; Argentine Basin (1971), transect shelf slope break to abyss, R.V. 'Atlantis II'; Guiana Basin (1972), transect shelf slope break to abyss, R.V. 'Knorr'; West European Basin (1972), between Ireland and Woods Hole, R.V. 'Chain'; 5) Scottish Marine Biological Association (1973–86), Rockall Trough, R.R.S. 'Challenger'; 6) Naval Ocean Research and Development Activities N.S.T.L. Station, U.S.A. (1981), Venezuela Basin, USNS 'Barlett'.

The vast majority of samples were obtained using various forms of epibenthic sledge (ES/ET/ED). The remaining samples were obtained using a Sanders Dredge (SD), Agassiz Trawl (AT), Anchor Dredge (AD), Otter Trawl (OT), Anchor Box Dredge (ABD), Spade Box Corer (SBC) and Beam Trawl (CP = chalût à perche). The samples were elutriated on board using sieves (mesh 0.42 mm USA and U.K., 0.25 & 0.50 mm France), fixed in 4% or 10% formal

saline (4% formaldehyde in the case of S.M.B.A. samples) and then after 24 hours, washed and transferred to 70% or 95% ethanol.

Histological Procedures

For taxonomic comparison, distortion of the sections had to be reduced to a minimum. Much distortion occurs with excessive heat during wax infiltration and section flattening. This was minimized by using low melting point polyester wax (37°C) (Steedman, 1957). This wax is miscible in alcohol and obviates the need to use xylene prior to hydration thus further reducing distortion. Most sections were cut at 25 microns, below this they fail to expand to their original proportions during flattening process (Aumonier, 1938). Standard, Mayer's haematoxylin was used with eosin as a counter stain and supplemented by sections stained with Azan to differentiate between acidophilic and basophilic cytoplasm (Humason, 1967). for muscle and connective tissue, the trichrome staining methods of Pantin, (1946) and Pollak, (1944) were used.

Three-dimensional reconstruction requires a sequence of perfectly alignable serial sections. At least two static reference points are necessary and which run the length of the embedded specimen. The technique of Pusey, (1939) was found to be the most satisfactory. The block was painted with an indelible colloidal stain made up of Indian ink and bile salts. The procedure has been used mainly to determine configuration of the coils of the hindgut.

Stained whole mounts were also prepared using Ehrlich's haematoxylin.

Shape Analysis: Specimens from nine abyssal Atlantic Basins were drawn in lateral view using a Wild M5 microscope with a drawing attachment. In the case of large samples specimens were selected randomly by spreading them over graph paper and then selecting them by X, Y co-ordinates specified by computer-generated random numbers. Using a Hewlett Packard Shape Analysis System the drawings were analysed with reference to the area and perimeter of each shape. Then, a series of linear measurements were made (Fig. 1), quantifying nine variables in each specimen. A further 'dummy' variable was added recording the presence or not of external radial shell markings. Analysis was by computer-based statistics. Standardization of the data to z-scores was achieved by substracting the mean (X) from each variate (Y) and dividing by the standard deviation (S) to give the rth standardized value

$$Zr = (Yr - X)/S$$

The data set so derived has a mean of zero and a standard deviation of one. In morphometric terms this transformation has three advantages. First, all values less than the mean have a negative sign and all greater are positive, with the result that distance (or degree of similarity) between individuals can be inspected visually. Second, it is possible to relate the distance from one individual to another or from one individual to a point of reference, (eg. a centroid) independent of the unit of measurement of the original data. Third, for multivariate analysis it is an advantage to have a standard variance of one in that each variable is on the 'equal footing' in a geometrical sense such that each variable is treated symmetrically and independent of the variance. It also was found that because the range in size of the specimens was
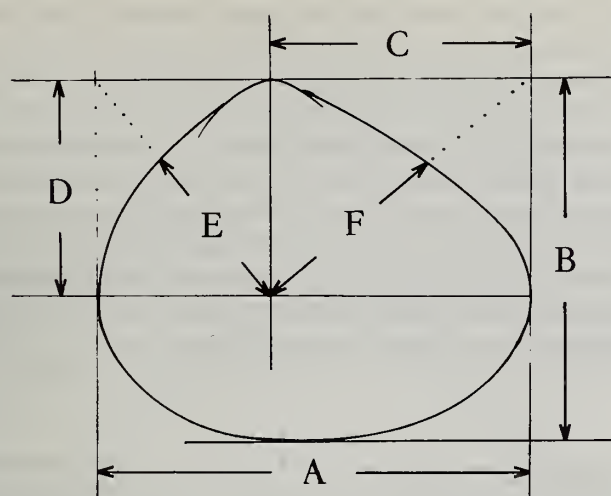
Fig. 1 Measurements (mm) A, B, C, D, E, F & G together with the area perimeter length for each specimen.

large it was necessary to eliminate a size effect by dividing each linear variable by length, and area by length squared. This is important because if shape differences are subtle (as many are) then size will tend to predominate in any clustering procedure and clusters will form on the basis of size rather than shape.

The morphometric data was subjected to multivariate analysis using the ordination technique of principal co-ordinate analysis (Gower, 1966). This was carried out using the software package GENSTAT on the Edinburgh University mainframe computer. Like principal component analysis, principal co-ordinates analysis is used to reduce dimensionality but, instead of being based on a P × P dispersion or correlation matrix where there are measurements on P variates for each of N individuals, it is based on an N × N association matrix and is therefore a Q rather than an R technique (Sokal & Sneath, 1963). The procedure generates a set of vectors that are a linear combination of the individuals scores. These are the principal co-ordinates. If the first K principal co-ordinates give an adequate representation of the data in K dimensions, the remaining N–K can reasonably be disregarded as uninformative.

Abbreviations to text figures

aa	anterior adductor muscle
apr	anterior pedal retractor muscle
by	'byssal' gland
cg	cerebral ganglion
dd	digestive duct
dh	dorsal hood
di	digestive diverticula
ft	foot
ga	gill axis
gi	gill
gs	gastric shield
ht	heart
hy	hypobranchial gland
ky	kidney
ma	mantle
oe	oesophagus
ov	ovary
pa	posterior adductor muscle
pb	palp proboscis
pg	pedal ganglion
pp	palp
ppr	posterior pedal retractor muscle
ps	posterior sorting area
sr	sorting ridges
ss	style sac
st	stomach
ts	testis
ty	typhlosole
vg	visceral ganglion

TAXONOMY

Early systematic studies on the Nuculidae (eg. Montagu, 1808; Reeve, 19885; Adams, 1856) were based on differences in shell morphology. A more-detailed attempt was made by Schenck, (1939) who also classified Recent and fossil species by shell characters alone, though he pointed out that it was impossible to say what characters should be accorded the greater weight, and whether emphasis should be placed on 'soft or hard part' morphology. Moore, (1931a, 1931b) distinguished between shallow-water nuculid species on the basis of the pattern of grooves on the faecal pellets, however Allen, (1954) was to show that this was not an infallible method. Indeed, sections of the hindgut show that the pellets of deep-sea species have no systematic value usually being round or oval in cross-section and without distinctive grooves. Heath, (1937) described variations in the musculature and the digestive system of various species and found that the configuration of the hindgut could be used as a consistent diagnostic feature. This remains true (Allen, 1978), however the hindgut of deep-sea nuculid species is usually smaller in diameter and far more extensively coiled as compared with shallow-water species, and to determine differences, delicate dissection is required, supported by examination of small whole-mount specimens and sections. Furthermore, there appears to be a degree of intraspecific variation. The musculature of deep-sea species *per se* has little systematic value but differences in the orientation of the body and the size and shape of the foot are reflected in the deposition of the pedal musculature. Interspecific differences in the morphology of the stomach were also noted.

Morphological orientation in bivalves is frequently related to a series of axes, (Allen, 1985). Definitions are by no means consistent, thus, Fischer, (1886) defined the antero-posterior axis as a straight line touching the lower margins of the adductor muscles, whereas, Jackson, (1890) considered it to pass through the mouth and the middle of the posterior adductor muscle. The cardinal or hinge axis as distinct from the body axis is most used as the basic criterion for orientation, the latter being assessed by the change from parallel of the hinge and oro-anal axes (Kauffmann, 1969). Unfortunately, the hinge axis is not easily determined in the Nuculidae. Differing orientations of the foot appear to be correlated with the degree of alignment of the adductor muscle axis as compared with the axis through cerebral and pedal ganglia (Fischer, 1886). Such axes cannot be determined with mathematical precision and cannot be used in a strict taxonomic sense, nevertheless they show how interspecific transformations are related to various anatomical reference points.

The family is very conservative with regard to its body

anatomy. Thus, Schenck, (1944) working with *Nucula tamat-avica* and Heath, (1937) with *N. nucleus* found that these species could not be separated from others on the basis of their anatomy. Similarly Moore, (1931a) and Allen, (1954) could not find any significant anatomical differences between the British species of *Nucula*. Shell morphology, therefore, remains of paramount importance to the taxonomy of the Nuculidae.

On the basis of shell morphology, Schenck, (1934) split the nuculids into three main 'Taxonomic Units'.

(A)   Forms with crenulate inner ventral margins.
       (1) *Nucula* Lamarck, (1799)
       (2) *Pronucula* Hedley, (1902)
       (3) *Pectinucula* Quenstedt, (1930)
       (4) *Linucula* Marwick, (1931)
       (5) *Deminucula* Iredale, (1931)
       (6) *Lamellinucula* Schenck, (1944)
       (7) *Gibbonucula* Eames, (1951)

(B)   Forms with smooth inner ventral margins.
       (1) *Ptychostolis* Tullberg, (1991)
       (2) *Nuculoma* Cossmann, (1907)
       (3) *Nuculopsis* Girty, (1911)
       (4) *Nuculoidea* Williams & Breger, (1916)
       (5) *Nuculopsis* Woodring, (1925)
       (6) *Leionucula* Quenstedt, (1930)
       (7) *Palaeonucula* Quenstedt, (1930)
       (8) *Ennucula* Iredale, (1931)
       (9) *Brevinucula* Thiele, (1934)
       (10) *Austronucula* Powell, (1939)
       (11) *Trigonucula* Ichikawa, (1949)
       (12) *Habonucula* Singh & Kanjilal, (1977)
       (13) *Condylonucula* Moore, (1977)

(c)   Forms with divaricate sculpture.
       (1) *Acila* H. & A. Adams, (1958)
       (2) *Truncacila* Schenck, (1931)

Thereafter, Cox, (1940) described species such as *Nucula obliqua* Lamarck, *Nucula expansa* Reeve and *Nucula superba* Hedley, as intermediate between 'crenulate' and 'non-crenulate' forms in that they possessed very fine crenulations only visible with microscopic aid. Vokes, (1949) who found a similar condition in the Palaeozoic species *Nuculoidea opima* Hall suggested that such species should be placed in a separate group.

Many of the taxa listed above, are known only as fossils. Of these Thiele, (1934) was of the opinion that *Ennucula* and *Leionucula* are congeneric and Allen & Hannah, (1986) synonymized *Linucula* with *Nucula*, ajudged that *Pronucula* is a subgenus of *Nucula* and that *Nuculopsis* Woodring (*non* Girty), *Leionucula*, *Ennucula* and *Austronucula* are synony-mous with *Nuculoma*.

On the basis of shell structure, Recent non-divaricate species have been divided into two genera, *Nucula* and *Nuculoma* (Poel, 1955). species in which the outer shell layer is constructed of radial elements and, consequently, have a crenulate inner ventral shell margin are included in the genus *Nucula*. Those with a uniform, non-radial, structure with a smooth inner ventral shell margin are included in *Nuculoma*. Taylor *et al.*, (1969) describe the shell of *Nucula* as being composed of three layers of aragonite, the inner being nacrous. Unfortunately, Taylor *et al.*, (1969) did not report on *Nuculoma*, however, we can confirm that *Nuculoma*

species described here have an inner nacrous layer. It has been assumed that species of the Nuculacea and Nuculanacea can be distinguished on the basis that nuculaceans have an inner nacreous layer, which is absent in nuculanceans, how-ever, Moore (1977) in his description of a tropical, shallow-water nuculacean *Condylonucula* states it is without an inner nacreous layer. Similarly Cox, (1959) states that early fossil members of the Nuculacea and Nuculanacea are not easily distinguished in that some Jurassic species of *Nuculana* have an inner nacreous layer. All deep-sea nuculaceans so far examined have an inner nacreous layer.

CLASSIFICATION

As a result of this study on the shell morphology and anatomy of the Nuculidae of the deep Atlantic and on the Recent and fossil material from the Natural History Museum, London (BM(NH)) and elsewhere, and examination of descriptions in the literature, a new listing of the *extant* genera of the family Nuculidae has been arrived at.

Family **NUCULIDAE** Gray, 1824

Genus **NUCULOIDEA** Williams & Breger, 1916

TYPE SPECIES: **Cucullea opima** Hall, (1843)
Shell ovate, inequilateral with concentric sculpture; faintly prosogyral; inner ventral margin not crenulate but with internal marginal micropectinations; resilifer perpendicular to hinge plate; inner nacreous layer present.

Originally Williams & Breger, (1916) proposed the subge-neric name *Nuculoidea* for Palaeozoic species of *Nucula* having a non-crenulate inner ventral margin and with other characters intermediate between those of the extinct family Ctenodontidae and the Recent members of the family Nucul-idae. These latter include a cartilage pit as found in *Cteno-donta albertina* Ulrich (upper Ordovician). Williams & Breger, (1916) divided the species of *Nuculoidea* into three groups each based on a described species: (1) *Nuculoidea opima* (Hall) with umbones twisted to a vertical position or faintly prosogyrate, shell usually anteriorly elongate and semi-lunate; (2) *Nuculoidea aquisgranensis* (Beuschausen) with opisthogyrate umbones, anterior and convexly rounded and usually the larger, posterior outline semi-lunuliferous; (3) *Nuculoidea niotica* (Hall) with opisthgyrate umbones, posterior margin truncate and nearly vertical, anterior margin also nearly straight, producing a characteristic vertically triangular outline. Later, McAlester, (1962) upgraded *Nucu-loidea* to generic rank. Similarly, Soot-Ryen, (1964) and Liljedahl, (1983, 1984) in a systematic account of nuculoid pelecypods from the Silurian (Palaeozoic) formations of gotland described a number of nuculoids with characters common with the *Nuculoidea opima* group and raised these species to the generic rank.

We are reluctant to create a new genus for Recent forms that match the description given above, particularly in regard to the faintly prosogyral nature of the beaks, the micropecti-nate margin and the vertical ligament. Furthermore, this relates to the fact that many deep-sea bivalves belong to groups with a long geological record.

Genus NUCULOMA Cossmann, 1907

TYPE SPECIES: **Nucula castor** d'Orbigny, (1850)
Shell ovate or triangular, smooth or with concentric sculpture; opisthogyral; ventral margin not crenulate as seen externally but may be microscopically crenulate internally corresponding with marginal limits of radial shell elements; resilifer oblique to hinge plate; inner nacrous layer present.

Cossmann, in Cossmann & Thiery, (1907) proposed the subgeneric name *Nuculoma* for Jurassic nuculids characterized for the most part by a narrow oblique chondrophore. Later Schenck, (1934) raised *Nuculoma* to generic rank.

Genus BREVINUCULA Thiele, 1934

TYPE SPECIES: **Nucula guineensis** Thiele, (1931)
Shell deeply triangular with smooth surface; opisthogyral; inner ventral margin not crenulate; resilifer absent or very small, inner nacrous layer present.

Thiele, (1934) originally proposed the subgeneric name *Brevinucula* for a deep-sea species *Nucula guineensis* (p. 83) from the Gulf of Guinea which was later synonymized with *Nucula verrilli* (Verrill & Bush, 1898).

Genus CONDYLONUCULA Moore, 1977

TYPE SPECIES: **?Condylonucula cynthiae** Moore, (1977)
Shell very robust, ovate with concentric sculpture, heavily sculptured cap-like prodissoconch; opisthogyral; inner ventral margin not crenulate; resilifer perpendicular to hinge plate; inner nacreous layer absent.

Species of *Condylonucula* are confined to shallow-water sediments of the tropical western Atlantic.

Genus NUCULA Lamarck, 1799

TYPE SPECIES: **Arca nucleus** Linné, (1758)
Shell ovate-triangular, inequilateral with reticulate sculpture; opisthogyral; inner ventral margin crenulate; hinge line angulate; resilifer oblique to hinge plate; inner nacrous layer present.

Genus DEMINUCULA Iredale, 1931

TYPE SPECIES: **Nucula praetenta** Iredale, (1931)
Shell triangular with reticulate sculpture; opisthogyral; inner ventral margin crenulate; hinge line angulate; resilifer not well-defined, inner nacrous layer present.

Schenck, (1934) questioned whether *Deminucula* should be included in the *Nuculidae* in that the original specimens (Smith, 1891) showed that they were without a 'chondrophore'. A possible explanation of the difference between *Deminucula* and *Nucula* is that there has been retention of juvenile shell characteristics into adulthood (neoteny) in *Deminucula* (p. 67). This is evident when *D. atacellana* is compared with the juveniles of a shallow water species such as *Nucula sulcata*.

Genus PRONUCULA Hedley, 1902

TYPE SPECIES: **Pronucula decorosa** Hedley (1902)
Shell triangular with reticulate sculpture; opisthogyral; inner ventral margin crenulate; hinge line arched; resilifer perpendicular to hinge plate, inner nacrous layer present.

This genus differs from *Nucula* in having an arched instead of an angulate hinge line, the hinge teeth series do not overlap beneath the umbos, and the resilifer is perpendicular rather than oblique to the hinge plate. Since the description by Hedley, (1902), Cotton, (1930) and Marwick, (1931) and Clarke, (1961) have described several other Recent and Tertiary species from the southern hemisphere.

Genus ACILA (Adams & Adams, 1858)

TYPE SPECIES: **Nucula divaricata** Hinds, (1843) Shell ovate-triangular with divaricate sculpture; opisthogyral; hinge line arched; inner ventral margin crenulate; resilifer oblique to hinge plate; inner nacrous layer present.

Adams & Adams, (1858) proposed the generic name *Acila* for nuculid species mainly characterized by a divaricate sculpture. Extant species are restricted to the Indo-Pacific and to relatively shallow depths (Schenck, 1934).

ATLANTIC DEEP-SEA SPECIES OF THE FAMILY NUCULIDAE

Deminucula atacellana (Schenck, 1939)

Figs 2–4, 5a, 6, 7a

TYPE LOCALITY: Porcupine St 16, off NW Coast of Ireland, 1476 and 1215 fms. Designated Schenk (1939).

TYPE SPECIMEN: Holotype: not designated, Lectotype: USNM No. 197154 selected by Schenck, (1939) Pl. 5, figs. 4, 5, 9, 10, 13, 16. (7 specimens from Atlantis II, Sta. 131, 39°38.5'N. 70°36.5'W, 2178 m lodged in BM(NH) No. 1990010). *Nucula reticulata* Jeffreys, 1876, p. 429; 1879, p. 583; (*non* Hinds, 1843); Smith, 1885, p. 229.

Nucula cancellata Jeffreys, 1881, p. 951; (*non* Meek & Hayden, 1856, p. 85); Verrill, 1884, p. 280, 285; Dall, 1890, p. 258; Dautzenberg & Fischer, 1897, p. 203, 204; Verrill & Bush, 1897, p. 854, pl. 81, Fig. 3, pl. 86, Fig. 5; Johnson, 1934, p. 15; Dautzenberg, 1927, p. 288.

Nucula (Nucula) atacellana Schenck, 1939, p. 27, pl. 5, Figs 4, 5, 8, 10, 13, 16.

DEPTH RANGE: 1102–4938 metres.

MATERIAL

Cruise	Sta	Depth (m)	No	Lat	Long	Gear	Date
				NORTH AMERICA BASIN			
Atlantis II	62	2496	82	39°16.0'N	70°33.0'W	ET	21.08.64
	64	2886	1	38°46.0'N	70°06.0'W	ET	21.08.64
	73	1470	361	39°46.5'N	70°43.3'W	ET	25.08.64
Chain	76	2862	1	39°38.3'N	67°57.8'W	ET	29.06.65
	77	3806	54	38°00.7'N	60°16.0'W	ET	30.06.65
	78	3828	12	38°00.8'N	69°18.7'W	ET	30.06.65
	85	3834	69	37°59.2'N	60°26.2'W	ET	5.07.65
	87	1102	48	39°48.7'N	70°40.8'W	ET	06.07.65
	87	1102	48	39°48.7'N	70°40.8'W	ET	06.07.65

Cruise	Sta	Depth (m)	No	Lat	Long	Gear	Date
Atlantis II	115	2051	2131	39°39.2'N	70°24.5'W	ET	16.08.66
Atlantis II	126	3806	3	39°37.0'N	66°47.0'W	ET	24.08.66
	128	1254	12	39°46.5'N	70°45.2'W	ES	16.12.66
	131	2178	1022	39°38.5'N	70°36.5'W	ES	18.12.66
Chain	210	2064	409	39°43.2'N	70°49.5'W	ES	22.02.69
	335	3882	3	40°23.3'N	46°30.0'W	ES	31.08.72
Knorr	340	3264	25	38°14.4'N	70°20.3'W	ES	24.11.73

WEST EUROPEAN BASIN

Cruise	Sta	Depth (m)	No	Lat	Long	Gear	Date
Chain	313	1500	15	51°32.2'N	12°35.9'W	ES	17.08.72
	316	2209	531	50°57.7'N	13°01.3'W	ES	18.08.72
	318	2506	7	50°27.3'N	13°20.9'W	ES	19.08.72
	321	2890	4	50°12.3'N	13°35.8'W	ES	20.08.72
Incal	CP08	2644	1	50°14.7'N	13°13.5'W	CP	27.07.76

ROCKALL TROUGH

Cruise	Sta	Depth (m)	No	Lat	Long	Gear	Date
Challenger	2	2857	2	55°04.0'N	12°33.0'W	ES	04.06.73
	3	1997	1	56°46.0'N	10°02.0'W	ABD	05.06.73
	4	1993	24	56°52.0'N	10°01.0'W	ES	05.06.73
	6	2900	547	55°02.0'N	12°29.0'W	ES	02.07.73
	8	2900	5	54°45.0'N	12°10.0'W	ES	03.07.73
	10	2540	147	56°37.0'N	11°04.0'W	ES	04.07.73
	12	2076	6	56°49.0'N	10°15.0'W	ES	20.09.73
	13	1842	8	56°45.0'N	09°50.0'W	ABD	22.09.73
	15	1632	13	56°44.0'N	09°28.0'W	ES	22.09.73
	18	1392	16	56°44.0'N	09°20.0'W	ES	22.09.73
	27	2880	456	54°40.0'N	12°16.0'N	ES	03.11.73
	34	2515	536	56°36.0'N	11°30.0'N	ES	10.05.75
	48	2875	1	55°04.0'N	12°04.0'W	SBC	07.09.75
	49	2875	1	55°03.0'N	12°05.0'W	SBC	07.09.75
	51	2875	1	55°03.0'N	12°03.0'W	SBC	07.09.75
	55	2878	52	54°40.0'N	12°16.0'W	ES	17.11.75
	56	2886	105	54°40.0'N	12°16.0'W	ES	01.03.76
	57	2950	67	54°41.0'N	12°23.0'W	ES	21.06.76
	58	2900	2	54°41.0'N	12°17.0'W	SBC	21.06.76
	59	2900	96	54°40.0'N	12°20.0'W	ES	21.06.76
	63	1800	1	56°37.0'N	09°49.0'W	SBC	25.06.76
	69	1050	24	59°39.0'N	07°12.0'W	ES	02.07.76
	110	2886	92	54°41.0'N	12°14.0'W	ES	22.10.76
	111	2886	104	54°40.0'N	12°16.0'W	ES	22.10.76
	118	2910	68	54°39.0'N	12°14.0'W	ES	28.01.77
	121	2910	1	54°37.0'N	12°09.0'W	AT	29.01.77
	124	2900	184	53°30.0'N	13°15.0'W	AT	30.01.77
	135	2900	158	54°39.0'N	12°16.0'W	ES	07.08.77
	137	2900	69	54°34.0'N	12°19.0'W	ES	22.02.78
	174	2885	1	54°44.0'N	12°18.0'W	SBC	22.05.80
	176	2245	168	57°15.0'N	10°26.0'W	ES	28.05.80
	185	2907	32	54°44.0'N	12°15.0'W	ES	10.04.81
	231	2898	69	54°42.0'N	12°12.0'W	ES	17.05.83
Incal	DS01	2091	3	57°59.7'N	10°39.8'W	SD	15.07.76
	DS02	2081	1	57°58.8'N	10°48.5'W	SD	16.07.76
	CP03	2466	4	55°38.0'N	11°64.4'W	CP	17.07.76
	CP04	2483	5	56°33.2'N	11°11.3'W	CP	17.07.76
	DS06	2491	24	56°26.6'N	11°10.5'W	DS	18.07.76
	DS07	2884	37	55°00.0'N	12°31.0'W	SD	19.07.76
	CP05	2884	4	55°00.0'N	12°29.0'W	CP	19.07.76
	CP06	2888	4	55°02.3'N	12°40.3'W	CP	19.07.76
	CP07	2895	4	55°03.4'N	12°49.2'W	CP	20.07.76
	DS09	2897	62	55°07.7'N	12°52.6'W	SD	20.07.76
	CP08	2644	1	50°14.7'N	13°13.5'W	CP	27.07.76

BAY OF BISCAY

Cruise	Sta	Depth (m)	No	Lat	Long	Gear	Date
Sarsia	S44	1739	14	43°40.8'N	03°35.2'W	ES	16.07.67
	S50	2379	1	43°46.7'N	03°47.8'W	ES	18.07.67
	S65	1922	3	46°15.0'N	04°50.0'N	ES	25.07.67
Biogas II	DS32	2138	2	47°32.2'N	08°05.3'W	SD	18.04.73
Biogas III	DS37	2110	1	47°31.8'N	08°34.6'W	SD	24.08.73
	DS41	3548	1	47°28.3'N	09°07.2'W	SD	26.08.73
	DS49	1845	29	44°05.9'N	04°15.6'W	SD	01.09.73

Cruise	Sta	Depth (m)	No	Lat	Long	Gear	Date
Biogas IV	DS50	2124	1	44°08.9'N	04°15.9'W	SD	01.09.73
	DS51	2430	5	44°11.3'N	04°15.4'W	SD	18.02.74
	DS52	2006	30	44°06.3'N	04°22.4'W	SD	18.02.74
	DS62	2175	1	47°32.8'N	08°40.0'W	SD	26.02.74
	DS63	2126	1	47°32.8'N	08°35.0'W	SD	26.02.74
	DS64	2156	3	47°29.2'N	08°30.7'W	SD	26.02.74
Biogas V	CP07	2170	7	44°09.8'N	04°16.4'W	CP	21.06.74
Biogas VI	DS71	2194	3	47°34.3'N	08°33.8'W	SD	20.02.74
	DS86	1950	105	44°04.8'N	04°18.7'W	SD	31.10.74
	DS87	1913	79	44°05.2'N	04°19.4'W	SD	01.11.74
	DS88	1894	7	44°05.2'N	04°15.7'W	SD	01.11.74
Polygas	DS18	2138	1	47°32.2'N	08°44.9'W	SD	22.10.72
	DS25	2096	5	44°08.2'N	04°15.7'W	SD	01.11.72
	DS26	2076	12	44°08.2'N	04°15.0'W	SD	01.11.72

GUYANA BASIN

Cruise	Sta	Depth (m)	No	Lat	Long	Gear	Date
Knorr	293	1518	9	08°58.0'N	54°04.3'W	ES	27.02.72
	299	2076	2	07°55.1'N	55°42.0'W	ES	29.02.72
	301	2500	12	08°12.4'N	55°50.2'W	ES	29.02.72
	303	2953	7	08°28.8'N	56°04.5'W	ES	01.03.72

CANARIES BASIN

Cruise	Sta	Depth (m)	No	Lat	Long	Gear	Date
Discovery	6697	1564	3	27°57.0'N	13°46.0'W	ED	15.03.68
	6701	1934	6	27°45.2'N	14°13.0'W	ED	16.03.68
	6704	2129	14	27°44.9'N	14°25.0'W	ED	17.03.68

CAPE VERDE BASIN

Cruise	Sta	Depth (m)	No	Lat	Long	Gear	Date
Atlantis II	141	2131	3	10°30.0'N	17°51.5'W	ES	05.12.67
	142	1796	48	10°30.0'N	17°51.5'W	ES	05.12.67
	148	3828	1	10°37.0'N	18°14.0'W	ES	07.12.67
	149	3861	2	10°30.0'N	18°18.0'W	ES	07.02.67

GUINEA BASIN

Cruise	Sta	Depth (m)	No	Lat	Long	Gear	Date
Walda	DS20	2514	1	02°32.0'S	08°18.1'E	SD	–
	DS29	3547	2	02°57.0'S	04°28.1'E	SD	–

ANGOLA BASIN

Cruise	Sta	Depth (m)	No	Lat	Long	Gear	Date
Atlantis II	195	3797	20	14°50.0'S	09°54.0'E	ES	19.05.68
	196	4630	6	10°29.0'S	09°04.0'E	ES	21.05.68
	197	4595	34	10°04.0'S	09°04.0'E	ES	21.05.68
	198	4566	16	09°47.0'S	10°29.0'E	ES	21.05.68
	200	2754	1	09°43.5'S	10°57.0'E	SD	22.06.68
	201	2031	8	09°05.0'S	12°17.0'E	ES	23.05.68

ARGENTINE BASIN

Cruise	Sta	Depth (m)	No	Lat	Long	Gear	Date
Atlantis II	243	3822	213	37°36.8'S	52°23.6'W	ES	14.03.71
	245	2707	77	36°55.7'S	53°01.4'W	ES	14.03.71
	256	3917	356	37°40.8'S	52°19.3'W	ES	24.03.71
	259	3305	862	37°13.3'S	52°45.0'W	ES	26.03.71

SHELL DESCRIPTION

The original description by Jeffreys, (1876) is detailed and accurate and only a summary description is given here.

Shell ovate, ventricose, lustrous, transluscent, equivalve, inequilateral; umbo posterior to midline, slightly opisthogyrate or orthogyrate; when postero-dorsal margin is orientated vertically the antero-dorsal margin is above horizontal; lunule and escutcheon not obvious, hinge teeth often visible through thin dorsal area; surface with fine concentric ridges which disappear towards the umbo, radial striations give impression of reticulation; chondrophore absent, resilifer inconspicuous, not oblique; hinge plate moderately broad; teeth chevron-shaped, the number varies with the size of the specimen (Fig. 2). Thus a shell 3.86 mm in length has 8 teeth in the anterior series and 5 in the posterior and for shells of 2.64 mm and 1.46 mm in length the numbers of teeth are 6/4 and 4/2 respectively.

There appears to be a continuous gradation in the external characters of *Deminucula atacellana* and of *Nucula callicre-*
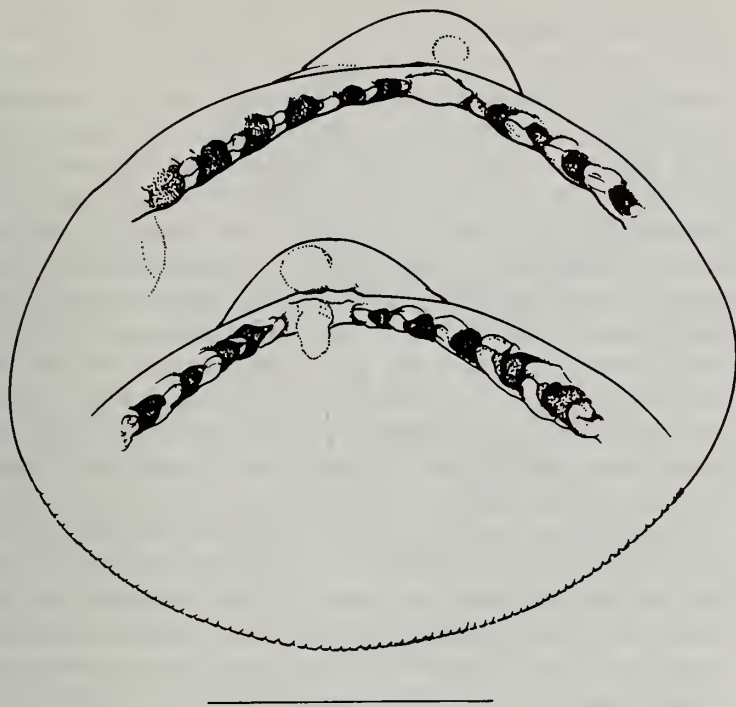
Fig. 2 *Deminucula atacellana*. Internal view of the left valve and hinge region of the right valve of a shell from Station 131. (Scale = 1.0 mm).
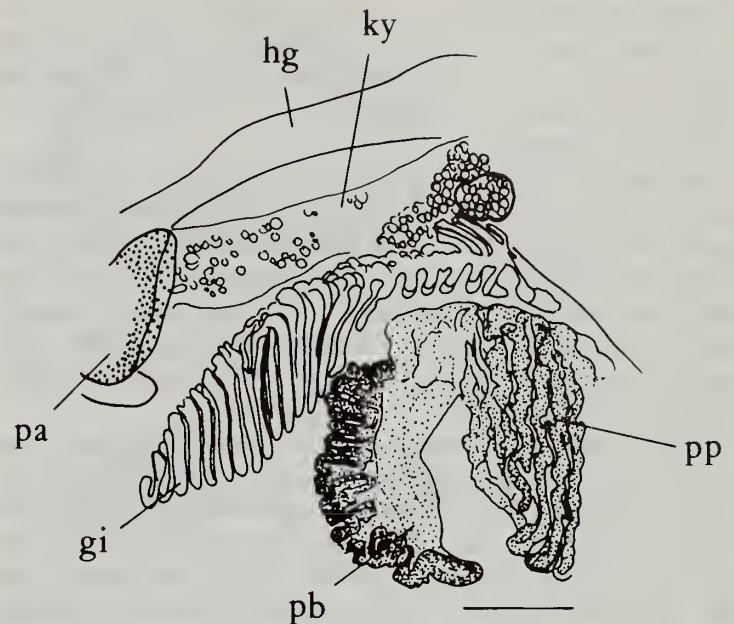

Fig. 4 *Deminucula atacellana*. Enlarged lateral view as seen from the right side of the gill and surrounding organs. (Scale = 0.2 mm; for key to abbreviations see p.63).

demna (Fig. 7b) (p. 69). While Dall, (1890) regarded *N. callicredemna* as belonging to the group which includes *D. atacellana*, both Schenck, (1939) and Knudsen, (1970) believed the species to be conspecific with *D. atacellana*. In contrast James, (1972) states that there is a change in the shape of the outline of *N. callicredemna* with age with the shell becoming more ovate. This allomorphic variation taken with the fact that adult populations of *D. atacellana* also show a large amount of variation in shape is probably the reason why authors have debated the species. In fact, some mature specimens of *D. atacellana* appear identical to small specimens of *D. callicredemna* however, small immature specimens of *N. callicredemna* do not look like large mature specimens of *N. callicredemna* nor of *D. atacellana* of similar length. The small immature *N. callicredema* are far more triangular in shape (James, 1972) (Fig. 7). Mature specimens of *N. callicredemna* and *D. atacellana* can be clearly sepa-

rated on the basis of the internal shell morphology, and apart from the features outlined in the shell descriptions of the two species, they also differ in that mature specimens of *D. atacellana* are typically deminuculoid and without a well-defined resilifer (Fig. 4), whereas mature specimens of *N. callicredemna* have a well-developed chondrophore (Fig. 8). *N. callicredemna* grows to a much larger size than does *D. atacellana*.
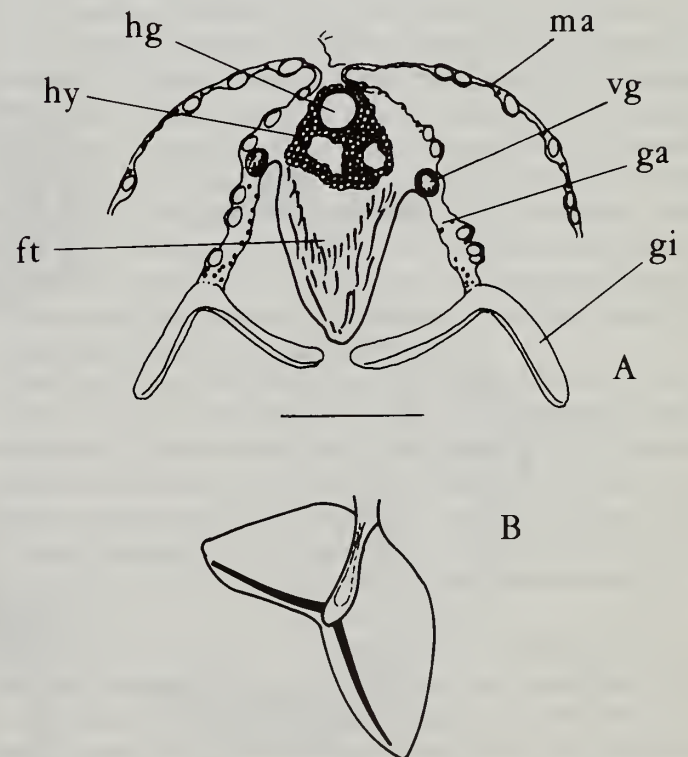

Fig. 3 *Deminucula atacellana*. The gross anatomy as seen from the right side of a whole mount with the shell removed. (Scale - 1.0 mm; for key to abbreviations see p.63).

Fig. 5 A. *Deminucula atacellana*. Semidiagrammatic view of a transverse section immediately anterior to the posterior adductor; B. *Nucula delphinodonta* inner and outer gill plates as drawn by Drew 1901. (Scale = 0.5 mm; for key abbreviations see p.63).

INTERNAL MORPHOLOGY

D. atacellana being the most common abyssal nuculid, is used to provide a basic account of morphology against which the other species can be described and compared. Particular emphasis is placed on features that show adaptation to its deep-water existence.

The mantle edge of *D. atacellana* is relatively unmodified and typically consists of an inner muscular lobe, a middle sensory lobe and an outer lobe which secretes the outer layer of the shell. The periostracum arises from the junction of the outer and middle layer and there is a broad zone of attachment of the pallial muscle. Trichrome staining shows numbers of gland cells scattered throughout the outer and inner epithelium of the mantle.

Each labial palp is made up of a proboscis, pouch and paired lamellae (Figs 3a & 4). They are not greatly larger in overall size to those of more shallow-water nuculid species (Allen, 1978) and their structure compares well with the description given by Hiraska, (1927) for *Nucula nucleus*. The inner surfaces are covered with a layer of columnar epithelial cells with long cilia and with a cytoplasm which is strongly acidophilic. The epithelial cells of the outer surfaces are squamous. The outer surfaces are smooth whilst the inner surfaces are ridged dorso-ventrally. The fine structure of the ridges compares well with that of *N. nucleus*. The ridges get smaller towards the anterior part of the palp and their structure in cross-section changes slightly. The number of ridges varies and ranges from 12 in specimens ca. 1 mm total length to 27 in specimens ca. 3 mm total length.

The palp proboscis extending from the posterior dorsal limit of the palps is muscular and contractile. The form in life is difficult to determine for in preserved specimens they are always in an extreme state of contraction (Fig. 4). Nevertheless, they have a similar morphology to that of *Nucula*

delphinodonta (Drew, 1901), and *Nucula nucleus* (Hirasaka, 1927). Morphologically they are an extension of the distal oral groove and a shallow V-shape in section. The concave surface and its margins consist of a single layer of columnar epithelial cells with long cilia. The convex surface has a single layer of more cuboidal epithelial cells whch appear to be devoid of cilia. Trichrome staining shows large numbers of mucous secreting cells, especially in the concave surface. Each proboscis has well-developed longitudinal muscle fibres amongst connective tissue. The fibres are continuous with the musculature of the body wall and are asymmetrically distributed so that on contraction the proboscis curls towards the concave surface. Each proboscis is supplied with a large nerve that originates in the cerebral ganglion and runs within the dorsal margin of the palps. There is also a large blood space. Palp pouches are features only found in the Nuculoidea. They are spoon-shaped and attached to the body at the point of attachment of the proboscis to the palp (Fig. 4). They establish continuity between the point of food collection and the distal oral groove of the palp. They have a simple structure consisting of two layers of cuboidal epithelium, separated by a thin layer of connective tissue. Within the latter is a material with similar staining properties to chitin. This material is also found in the gill plates where it forms the skeletal rods. Short cilia are present on the concave surface and margins of the pouch but not on the convex surface.

The gills are suspended obliquely from the postero-dorsal edge of the viscero-pedal mass across the posterior mantle cavity adjacent to the ventral margin of the posterior adductor muscle (Figs 3 & 4). The number of gill plates on the axis varies with the size of the specimen and ranges from 5 pairs in specimens ca. 1 mm in length to 24 pairs in mature specimens ca. 3 mm in length. Drew, (1901) found that 20 pairs was the common number in full grown specimens of the shallow-
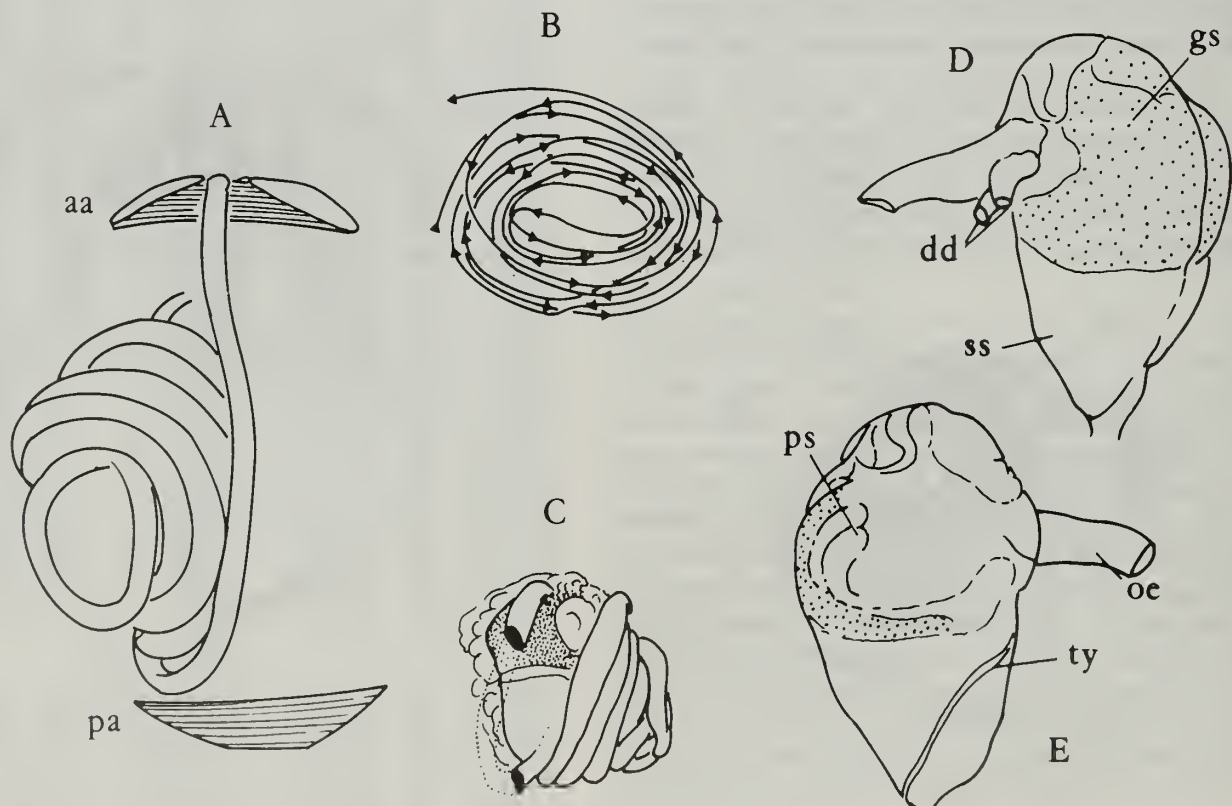

Fig. 6   *Deminucula atacellana*. A. Dorsal view of hind gut *in situ*; B. Course of hind gut as seen from right side—elucidated by dissection; C. Posterior view of stomach and hind gut—note a section of gut immediately posterior to the stomach is missing; D & E. Intact stomach as seen from the left and right side respectively. (Scale = 0.1 mm; for key abbreviations see p.63).
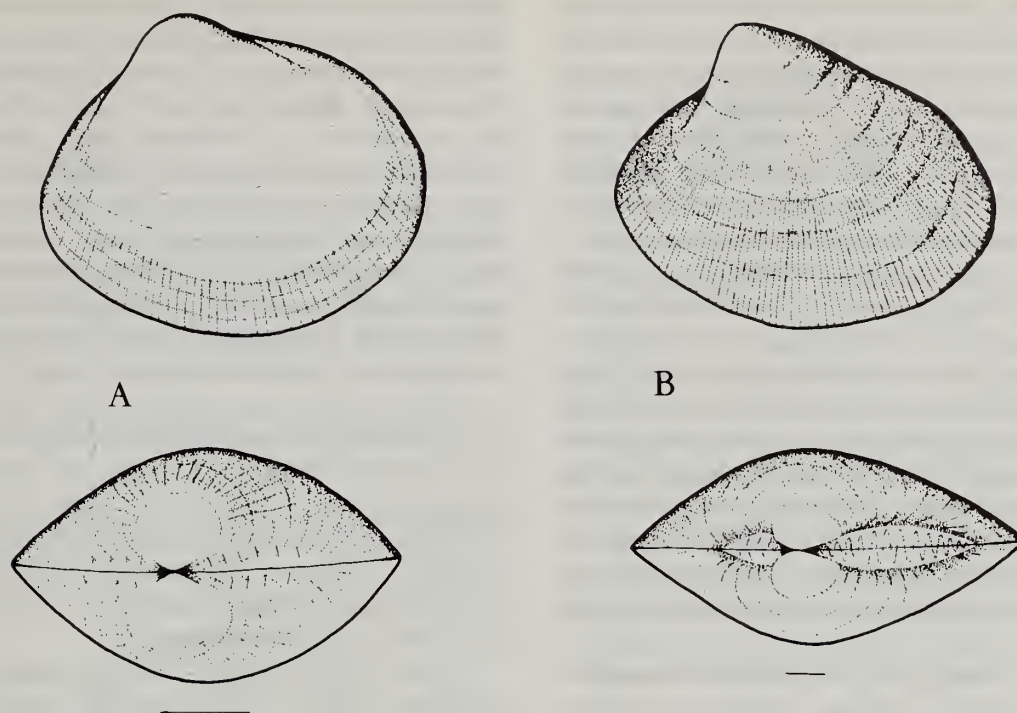
Fig. 7 A. *Deminucula atacellana* and B. *Nucula callicredemna*. A comparison of the external features of the two species as seen from right lateral and dorsal views. (Scales = 1.0 mm).

water species *Nucula delphinodonta* Mighels & Adams, 1842. The gill plates of *D. atacellana* have a different shape to those of *Nucula delphinodonta* (Figs 5a & b). In the latter case the plates are more triangular in shape. The finger-like plates of *D. atacellana* appear to be similar to those of *Nucula proxima*, another shallow-water species (Hampson, 1971), but when surface areas are compared, that of *D. atacellana* is less than half that of *N. proxima*. This may relate to the fact that deep-sea species have different respiratory requirements, but may also be a reflection of the small quantities of suspended material in deep water (Allen, 1978). Shallow-water species (eg. *N. nucleus*) may be facultative filter feeders (Caspers, 1940). The distal ends of the inner plates of each gill meet in the midline posterior to the foot. The gills of *D. atacellana* are supported by a skeletal framework, trichrome stain indicates that chitin occurs in the gill axis and in the ventral part of the gill plates. A few muscle fibres are present in the axis.

The nervous system of *D. atacellana* appears to be similar to that of *N. delphinodonta* (Drew, 1901). Cerebral ganglia are located on each side of the oesophagus and are connected by a short commissure that passes between the outer wall of the oesophagus and the anterior adductor muscle. From each cerebral ganglion there are two posteriorly directed commissures. The more dorsal passes through the viscera and joins with an elongate visceral ganglion anterior to the posterior adductor muscle. The ventral commissures extend into the foot to connect with the pedal ganglia. Adjacent and postero-dorsal to the pedal ganglia are a pair of statocysts which contain crystalline fragments, the statoliths. Cephalic sense organs (Vlès, 1905) are present on either side of the mouth close to the proximal palp ridge and immediately ventral to the cerebral ganglia and are innervated from the latter.

In *N. Nucleus* (Hirasaka, 1927) the cephalic sense organs comprise pigment cells with a cornea, in contrast to *D. atacellana* where there is a thickened epithelium which is innervated from the cephalic ganglia, but with no evidence of differentiation into cornea and pigment cells.

The hypobranchial gland (Pelseneer, 1891), consists of a layer of swollen columnar cells covering the surface of the suprabranchial cavity and the outer surface of the membrane suspending the gill axis (Fig. 5). The gland in *D. atacellana* is similar to that described for *Nucula delphinodonta* (Drew, 1901) and *Nucula turgida* (Yonge, 1939). According to Yonge, (1939) the function of the gland is to produce a secretion that binds any fine material which passes between the gill filaments into the suprabranchial cavity. In *Nucula delphinodonta* it has the additional function of forming a brood sac (Drew, 1901). Heath, (1937) believed that the gland produced different types of secretion in different species. In some species he found the gland stained deeply with Delafield's haematoxylin, whilst in others it remained unstained. In the case of *D. atacellana* different staining characteristics were found in different specimens. Sometimes it stained only with Orange G, sometimes with Aniline Blue, sometimes in part with Orange G and in part with Aniline Blue, and sometimes it would not take up any stain and remained colourless. The reasons for the apparent changing chemistry of this gland are unclear. Similarly the function of the gland is yet to be determined.

The foot has a similar shape and proportions to that of shallow-water species (Fig. 3). The sole is divided sagitally and there is a prominent heel. The margins of the sole are fringed with papillae. The number of papillae (c. 10) does not appear to vary with the size of the animal. A large, dorso-ventrally elongate, 'byssal' gland is present in the heel of the foot and from it a short duct opens at the posterior limit of the sole.

The pedal muscles of *N. delphinodonta* (Drew, 1901) are arranged in three pairs, two of which are attached antero-dorsally and the third postero-dorsally to the shell. The arrangement of *D. atacellana* differs from this and corresponds more closely with the arrangement in *Acila divaricata* (Heath, 1937). Thus, there is only one pair of anterior muscles lying immediately posterior to the oesophagus. Twin medial pedal muscles attach to each valve and then merge and pass to the outside of the stomach to serve the central

region of the foot. There is a pair of posterior pedal muscles which pass to either side of the hindgut. In *Acila divaricata* the anterior pair are the largest, (Heath, 1937). This is not the case in *D. atacellana*, where all are approximately equal in size. The mechanics of foot movement in the protobranchs was described by Driscoll, (1964). The median and posterior pedal muscles are retractors, the anterior pair which control the anterior movement of the foot are protractors. Heath, (1937) believed that the posterior part of the anterior muscles also acted as a retractor. The 'byssal' gland in the heel of the foot of protobranchs opens to the median groove of the foot, however, nothing comparable to byssus threads have been observed. Its structure differs greatly from the byssus gland of lamellibranchs and there is no evidence that it is a vestige of a post-larval gland (Heath, 1937). In the protobranchs it varies greatly in size in different species although it is fairly consistent in its composite structure. In *D. atacellana* it is comparatively large. The lumen of the gland may contain traces of a secretory material. The surrounding cells are usually swollen and vacuolated.

In general the form of the gut of *D. atacellana* compares well with descriptions given by Yonge, (1939) and Owen, (1956) for shallow-water species. The mouth is situated mid-ventrally a short distance behind the anterior adductor muscle (Fig. 3). At the point of its junction with the distal oral grooves it is laterally distended and bilobed in cross-section. The oesophagus enters the stomach antero-dorsally and a little to the left of the mid-line. This is in contrast to *Nucula sulcata* where the oesophagus enters the stomach to the right of the mid-line (Owen, 1956), however, in *D. atacellana* most of the right side of the body is occupied by the extremely elongate hindgut (see below). The oesophageal epithelium is much folded and is made up of a mixture of cuboid and columnar cells. The epithelial cells are richly ciliated and there are mucous cells present between them. There is a layer of subepithelial circular muscle that is progressively thicker towards the stomach, so much so that it probably forms a sphincter at the junction with the stomach. Functionally this is essential to prevent regurgitation of the stomach contents when under pressure.

The combined stomach and style sac consist of a dorsal globular region—the stomach proper—and a ventral conical tapering style sac (Fig. 6). The dorsal hood ('dorsal pouch' of Graham, 1949) extends along the left wall of the stomach to end blindly on the left dorsal side. As in most protobranchs three ducts enter the stomach anteriorly from the digestive diverticula. In *D. atacellana* there is one on the left and two adjacent to each other close to the mid-line and ventral to the oesophagus. There is no small caecum similar to that found on the right of the mid-dorsal line in the stomach of *N. sulcata* (Owen, 1956). A grooved ciliated sorting area which extends over most of the right side of the stomach is visible through the stomach wall. In a specimen approximately 3 mm long seven grooves are present. This compares with more than 25 in a specimen of *N. sulcata* 15 mm in length. A reduction in the number of the ciliated grooves is a consistent feature in deep-sea species. The left wall of the stomach is lined with a gastric shield and in the region of the dorsal hood this is thickened to form a pronounced tooth. Previously regarded simply as an inert structure serving to protect the underlying epithelium and assist in the trituration of the gastric contents, Halton & Owen, (1968) showed it has a far more elaborate structure and function. There are two components, an inner part consisting of numerous microvilli of underlying epithelial cells which extend into the secreted matrix and, an outer matrix of non-cellular chitin. At intervals on certain microvilli vescicular swellings are present. Histochemical studies show the shield to be enzymatically active. The epithelium underlying the shield is of columnar cells which are tallest in the region of the gastric tooth. Distally these cells are packed with pigment granules. Yonge, (1939) and Owen, (1956) suggest that they are probably excretory. Histochemical studies suggest they are related to lipofuschin pigments which are generally regarded as by-products of lipid metabolism. Underlying the epithelium of the stomach is a layer of collagen and a system of muscle fibres.

The hindgut is extremely long. This is characteristic of deep-sea nuculids and it is particularly elongate in *D. atacellana* (fig. 6). This may relate to the fact that deep-sea sediments make a poor diet with many of the organics resistant to digestion and therefore demanding of time for digestion, however, the discovery of complete forameniferans in the stomach perhaps indicate more *living* matter is ingested than was previously thought.

Heath, (1937) used the configuration of the hindgut as a diagnostic feature and found the simplest and possibly the most-primitive nuculoid configuration is that found in species of *Acila*. The more-complex extensive overlapping of the coils in *D. atacellana* makes the course of the gut difficult to determine except by three dimensional reconstruction (Fig. 6).

The digestive diverticula of *D. atacellana* consist of numerous blind-ending tubules which communicate with the stomach by a system of unbranched secondary ducts and much-branched main ducts. The main ducts are lined with cuboidal cells with a spherical or slightly oval nucleus and numerous pigmented cytoplasmic granules. Owen, (1956) in studies on living *N. sulcata* found these latter to be lipo-pigments staining strongly with Sudan Black B, suggesting that they were a bi-product of lipid metabolism and, from frozen sections, he confirmed the presence of lipids in the basal region. The cells are without cilia but have a well-developed brush border.

Secondary ducts in *D. atacellana* are similar to main ducts. This is in contrast to *N. sulcata* where secondary ducts have a dense coat of long cilia which extend almost to the centre of the lumen. While individual tubules of *N. sulcata* are round or oval in cross-section (Owen, 1956), those in *D. atacellana* are much more irregular. This appears to be a consistent feature in deep-sea protobranchs. Two types of cell occur. The most numerous have an irregular outline and are highly vacuolated. They contain two types of cytoplasmic granule, one large and blue staining and the other small and usually red in trichrome staining. The blue colour indicates an external membrane of basophilic mucus, the red colour indicates an acid mucopolysaccharide. A second, much less common, type of cell is present in small clusters scattered within the tubules. They are distinguishable by a lack of granules, a more-prominent nucleus and a more-darkly staining cytoplasm. They tend to be triangular in outline and distally narrow. According to Owen, (1956), they possess a single flagellum but this was not seen in *D. atacellana*. The dark staining cells have been regarded as excretory and secretory, but it remains unclear what function they perform (Owen, 1956). No evidence of intra-cellular digestion was seen and it is generally agreed that digestion in protobranchs is exclusively extra-cellular.

Studies of *D. atacellana* by Sanders and Hessler, (1969),

Scheltema, (1972) and Grassle & Sanders, (1973) from the North America Basin suggests this species has non-periodic reproduction. Preliminary evidence from samples taken in February, June, October and November from Biscay supports this view.

Sexes are separate and of equal proportions. Gonads are simple, paired, and overlie the viscera. The gonoducts open into the supra-branchial cavity. Maximum diameter of the ova is 135 μm. Approximately 200 ova are present in a specimen 3.3 mm total length. No brooding of the eggs occurs, development is probably lecithotrophic (Scheltema, 1972).

COMPARATIVE SHELL MEASUREMENTS OF SPECIMENS OF *D. atacellana*

Dimension (mm)	No.	Mean	SD	Max.	Min.
NORTH AMERICA BASIN					
Length	45	3.07	0.88	5.04	1.51
Width		1.88	0.57	3.23	0.94
Height		2.71	0.79	4.55	1.34
WEST EUROPEAN BASIN					
Length	77	2.96	1.14	4.87	0.78
Width		1.85	0.75	2.89	0.48
Height		2.58	0.96	4.02	0.76
BAY OF BISCAY					
Length	134	2.68	0.84	4.53	0.69
Width		1.67	0.56	2.96	0.45
Height		2.34	0.72	3.75	0.68
S.E. ATLANTIC					
Length	58	2.46	1.57	5.54	0.84
Width		1.42	0.93	3.33	0.45
Height		2.17	1.37	4.77	0.76
GUYANA BASIN					
Length	17	3.67	1.74	6.50	1.34
Width		2.04	0.99	3.75	0.75
Height		3.13	1.49	5.50	1.16
CANARIES BASIN					
Length	14	1.77	0.42	2.78	1.37
Height		1.05	0.24	1.64	0.83
Height		1.56	0.34	2.41	1.23
CAPE VERDE BASIN					
Length	7	2.26	0.73	3.49	1.46
Width		1.30	0.44	2.10	0.88
Height		1.95	0.60	2.92	1.29
ARGENTINE BASIN					
Length	23	3.50	1.10	5.20	1.14
Width		1.96	0.64	3.11	0.66
Height		3.18	1.00	4.74	1.05

DISTRIBUTION

D. atacellana is common and widespread. The species was originally described from specimens taken from the West European Basin by Jeffreys, (1881). It also was recorded from the North America Basin (Verrill, 1884), the Surinam Basin (Dall, 1890) and the Canaries Basin (Dautzenberg and Fischer, 1897). The species occurs throughout the North Atlantic, as far north as the Rockall Trough in the east and the Davis Strait in the west. In the South Atlantic it occurs in the Guinea, Angola and Argentine Basins but to date has not been taken from the Brazil Basin or the Sierra Leone Basin nor is it recorded by Clarke, (1961) in the Cape Basin. It appears to be absent from high latitudes—the Antarctic (Thiele, 1912; Dell, 1972), Arctic (Clarke, 1960; Bernard, 1979) and Norwegian Basins (Bouchet & Warén, 1979).

D. atacellana is the most eurybathic of the deep-sea nuculids with a vertical range of approximately 4000 m. It is not found in depths less than 1000 m. Shallow-water nuculids appear not to occur much beyond the continental shelf edge eg. Thus for European seas with the possible exception of *Nuculoma tenuis* and *Nucula tumidula* Malm shelf species which penetrate down slope to some degree, there appears to be little overlap of shelf and slope species at the extremities of their ranges. More sampling will be necessary to confirm this but there appears to be a gap between 200 m and 500 m in which few species of *Nucula* dominate. *D. atacellana* consistently occurs deeper in the Basins south of the equator than in the north. This may possibly relate to the absence of *Brevinucula verrilli* (p. 85) from the southern Basins.

Nucula callicredemna Dall, 1890

Figs 7b & 8

TYPE LOCALITY: Albatross Sta. 2754, Northeast of Tobago, Lat. 11°40′N., Long. 58°33′W, 1609 m.

TYPE SPECIMEN: Holotype. No holotype was designated. The type lot (USNM–95431) contained 11 valves, 1 conjoined specimen and several fragments (James, 1972). Re-examined (1991, JAA) 6 valves (4 in poor condition) and one conjoined specimen and fragments. Conjoined specimen selected as lectotype.

Nucula callicredemna Dall 1890, p. 258, pl. 31, Fig. 9; James 1972, p. 29, 34–36, Figs 5–14, map 2.
Nucula crenulata var. obliterata Dall 1886 p. 247, (in part); (*non N. crenulata var. obliterata* Dall, 1881).
Nucula obliterata Knudsen, 1970, p. 177; Pequegnat, 1972, p. 74.
Nucula aureliae Métivier, 1982, p. 39–42, Fig. 1, pl. 1, Figs 1–2.

DEPTH RANGE: 3411–4077 metres.

The taxonomy of this species is complicated by the fact that Dall, (1886) incorrectly identified a specimen of *N. callicredemna* (USNM. 63133) from 'Blake' Sta. 236 as *Nucula crenulata var. obliterata* (Knudsen, 1970). It is also possible that certain specimens in past records reported as *N. cancellata* (= *D. atacellana*) could be small specimens of *N. callicredemna* (p. 66). We believe that *Nucula aureliae* which Métivier, (1982) has described from 3360 metres off the Azores Archipeligo is synonymous with *N. callicredemna* and, if true, its range is now extended to the Canaries Basin. Métivier, (1982) who regarded *N. aureliae* as being similar to *N. cancellata* (= *D. atacellana*) failed to mention *N. callicredemna*. *N. callicredemna* also appears to be identical, certainly in shell morphology, to the Arctic deep-sea species *Nucula zophos* (Clarke, 1960), although this cannot be certain until the internal morphologies have been compared. Dall, (1890) also regarded *N. callicredemna* as being similar to the Pacific deep-sea species *Nucula niponica* (Smith, 1885).

N. callicredemna originally taken from off Tobago in 1609 metres (Dall, 1890) is now known to be common in the Gulf of Mexico in depths ranging from 2122 metres to 3563 metres (James, 1972). The one specimen taken off Recife in the Brazil Basin now extends the range of the species approximately 2180 km south.

MATERIAL

Cruise	Sta	Depth (m)	No	Lat	Long	Gear	Date
				BRAZIL BASIN			
Atlantis II	156	3459	1	00°46.0'S	29°28.0'W	ES	14.02.67
				GUYANA BASIN			
Knorr	306	3392	4	09°31.1'N	56°20.6'W	ES	02.03.72
				VENEZUELA BASIN			
Norda	33	3800–4035	1	15°08.0'N	69°12.0'W	OT	24.10.81
	35	3954–4017	16	15°08.0'N	69°12.0'W	OT	25.10.81
	36	3951–4044	24	15°08.0'N	69°12.0'W	OT	26.10.82
	37	3995–4097	11	15°08.0'N	69°12.0'W	OT	27.10.81
	38	3995–4013	15	15°08.0'N	69°12.0'W	OT	28.10.81
	39	3993–4065	1	15°08.0'N	69°12.0'W	OT	28.10.81
	40	3967–4009	11	15°08.0'N	69°12.0'W	OT	28.10.81
	87	3482–3518	22	13°30.0'N	64°45.0'W	OT	25.11.81
	88	3516–3550	25	13°30.0'N	64°45.0'W	OT	25–26.11.81
	90	3422–3464	19	13°30.0'N	64°45.0'W	OT	26–27.11.81
	91	3459–3503	12	13°30.0'N	64°45.0'W	OT	27.11.81
	92	3476–3518	34	13°30.0'N	64°45.0'W	OT	27–28.11.81
	93	3411–3459	21	13°30.0'N	64°45.0'W	OT	28.11.81
	94	3428–3476	11	13°30.0'N	64°45.0'W	OT	28–29.11.81

SHELL DESCRIPTION
The original shell description by Dall, (1890) is detailed, although as pointed out by James, (1972) it is in reverse ie. in the description anterior is posterior and *vice versa*. A summary description is given here.

Shell large, ovoid, lustrous, equivalve, inequilateral, surface covered in fine concentric ridges, radial striations give surface a fine reticulated appearance; umbos (frequently eroded) posterior to the midline, opisthogyrate; when posterior margin orientated vertically the anterior dorsal margin is above the horizontal; lunule long, escutcheon short and broad, dentition often visible dorsally through the shell, especially beneath the lunule; resilifer oblique to narrow hinge plate, extends ventral to anterior proximal teeth, teeth typically chevron-shaped but obtusely angled, number varies with the size of the specimen (6 posterior and 8 anterior teeth in a specimen 3.1 mm in length and 15 posterior and 29 anterior teeth in a specimen 18.9 mm in length (James, 1972), ligament tear-drop shaped.

Nucula callicredemna: MEASUREMENTS (FROM JAMES, 1972)

Sta.	V	L	H	B	A	P
6813–9	l	18.9	14.0	3.6	29	15
'	r	18.9	14.0	3.5	30	14
6787–4A	l	12.2	9.4	3.2	21	11
'	r	12.2	9.4	3.2	21	11
'	l	9.2	7.7	2.2	19	10
'	r	9.2	7.7	2.2	19	10
65A14–6	l	6.1	5.2	1.4	14	7
'	r	6.1	5.2	1.4	13	7
'	l	3.1	3.0	0.9	10	6
'	r	3.1	3.0	0.9	8	6

V = valve, r = right valve, l = left valve, L = length (mm), H = height (mm), B = breadth (mm), A = number of anterior teeth, P = number of posterior teeth.

Characteristically, *N. callicredemna* has a well-developed chondrophore that extends ventral to the anterior proximal teeth and is similar to that in shallow-water species such as *Nucula sulcata* (Fig. 8). It has similar proportions to that of many shelf species but the large size of the shell (19 mm total length), is unusual in a deep-sea species (James, 1972). It is by far the largest deep-sea nuculid in the Atlantic.

INTERNAL MORPHOLOGY
Discounting differences related to size the internal morphology is not greatly different from that of *D. atacellana*. The palp is large and deep covering much of the foot and in a specimen 16 mm total length there are 65–70 palp ridges. The gill is narrow lying diagonally across the posterior part of the mantle cavity. The axis is parallel to the postero-dorsal shell margin. The same specimen bears 32 gill plates. The course of the hind gut is similar to that of *D. atacellana*. There are fourteen ridges on the posterior sorting area of the stomach.
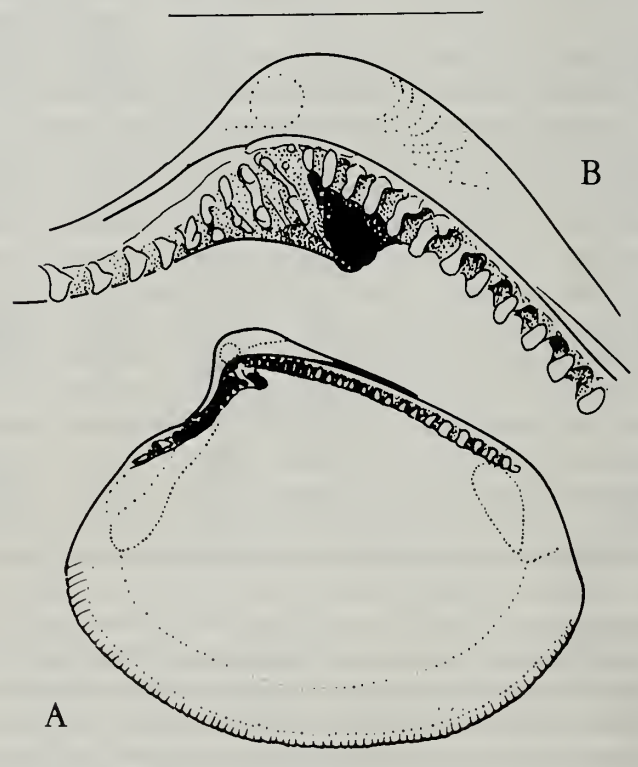

Fig. 8 *Nucula callicredemna*. A. Internal view of left valve; from Station 156; B. Detail of hinge of same valve. (Scales = 1.0 mm).

Nuculoidea bushae (Dollfuss, 1898)

Figs 9–11

TYPE LOCALITY: U.S. Bureau Fisheries Sta. 2171, Lat. 37°59'30"N, Long. 73°48'40"W.

TYPE SPECIMEN: Holotype: USNM No. 40474.

Nucula subovata Verrill & Bush, 1898, p. 858, pl. 81, Fig. 8; pl. 83, fig. 5; Johnson, 1934, p. 15; (*non* D'Orbigny, 1850).
Nucula bushi Dollfuss, 1898, p. 180.
Nucula bushae emend Schenck, 1939, p. 37.

DEPTH RANGE: 509–2876 metres.

MATERIAL

Cruise	Sta	Depth (mm)	No	Lat	Long	Gear	Date
			NORTH AMERICA BASIN				
Atlantis	D1	509	13	39°54.5'N	70°35.0'W	AD	23.05.62
Chain	105	530	235	39°56.6'N	71°03.6'W	ES	05.05.66
			WEST EUROPEAN BASIN				
Sarsia	S44	1739	67	43°40.8'N	30°35.2'W	ES	16.07.67
	S65	1922	1	46°16.5'N	04°44.0'W	ES	25.07.67
Chain	313	1500	46	51°32.2'N	12°35.9'W	ES	17.08.72
Chain	314	1015	42	51°54.6'N	12°27.3'W	ES	18.08.72
	316	2209	10	50°58.7'N	13°01.6'W	ES	18.08.72
Challenger	4	1993	85	56°52.0'N	10°01.0'W	ES	05.06.73
	12	2076	19	56°49.0'N	10°15.0'W	ES	20.09.73
	13	1842	93	56°45.0'N	09°50.0'W	ABD	22.09.73
	15	1632	32	56°44.0'N	09°28.0'W	ES	22.09.73
	18	1392	64	56°44.0'N	09°20.0'W	ES	22.09.73
	20	1271	336	56°46.0'N	09°17.0'W	ES	23.09.73
	22	1028	392	56°41.0'N	09°11.0'W	ES	23.09.73
	61	2000	1	57°08.0'N	12°09.0'W	SBC	23.06.76
	63	1800	6	56°37.0'N	09°49.0'W	SBC	25.06.76
	64	1400	2	56°39.0'N	09°29.0'W	SBC	26.06.76
	65	1600	5	56°39.0'N	09°40.0'W	SBC	26.06.76
	66	1200	2	56°39.0'N	09°23.0'W	SBC	26.06.76
	67	1000	1	56°39.0'N	09°13.0'W	SBC	26.06.76
	68	1800	2	58°42.0'N	09°43.0'W	SBC	01.07.76
	99	1160	264	60°00.0'N	10°35.0'W	ES	09.07.76
	105	1600	15	58°27.0'N	12°35.0'W	ES	10.07.76
	155	1330	6	48°27.0'N	10°20.0'W	SBC	04.08.79
	156	1310	6	48°27.0'N	10°21.0'W	SBC	05.08.79
	159	2036	3	50°55.0'N	12°21.0'W	SBC	08.08.79
	188	2876	1	54°40.6'N	12°16.1'W	SBC	15.08.81
	215	2001	2	57°02.0'N	09°47.0'W	SBC	03.08.82
	220	1608	8	59°05.0'N	08°51.0'W	SBC	04.08.82
	222	1101	15	59°43.0'N	07°43.0'W	SBC	05.08.82
	232	2105	8	57°17.0'N	10°16.0'W	ES	19.05.83
	272	2250	1	56°40.0'N	10°30.0'W	SBC	05.08.83
	273	2185	10	56°05.0'N	10°28.0'W	AT	05.08.83
	277	1593	1	56°16.0'N	09°44.0'W	SBC	06.08.83
Incal	DS02	2081	1	57°58.8'N	10°48.5'W	SD	16.07.76
	CP02	2091	3	57°58.4'N	10°42.8'W	SD	16.07.76
			BAY OF BISCAY				
Biogas I	DS11	2205	1	47°35.5'N	08°33.7'W	SD	08.08.72
Biogas III	DS49	1845	20	44°05.9'N	04°15.6'W	SD	01.09.73
	DS50	2124	3	44°08.9'N	04°15.9'W	SD	01.09.73
Biogas IV	DS52	2006	24	44°06.3'N	04°22.4'W	SD	18.02.74
Biogas V	CP07	2170	7	44°09.8'N	04°16.4'W	CP	21.06.74
Biogas VI	DS71	2194	1	47°34.3'N	08°33.8'W	SD	20.10.74
	CP24	1995	5	44°08.1'N	04°16.2'W	CP	31.10.74
DS86		1950	9	44°04.8'N	04°18.7'W	SD	31.10.74
	DS87	1913	14	44°05.1'N	04°19.4'W	SD	01.11.74
	DS88	1894	14	44°05.2'N	04°15.7'W	SD	01.11.74
Polygas	DS18	2138	1	47°32.9'N	08°44.9'W	SD	22.10.72
	DS25	2094	11	44°08.2'N	04°15.7'W	SD	01.11.72
	DS26	2076	11	44°08.2'N	04°15.0'W	SD	01.11.72
			GUYANA BASIN				
Knorr	295	1022	28	08°04.2'N	54°21.3'W	ES	28.02.72
			GUINEA BASIN				
Walda	DS28	1261	37	04°21.2'N	04°35.2'E	SD	00.00.71
			ANGOLA BASIN				
Atlantis II	203	542	22	08°48.0'S	12°52.0'E	ES	23.05.68
			CANARIES BASIN				
Discovery	6696	1780	3	28°06.0'N	13°28.0'W	ES	15.03.68
	6697	1564	2	17°57.0'N	13°46.2'W	ES	15.03.68
	6701	1934	12	27°45.2'N	14°13.0'W	ES	16.03.68
	6704	2129	17	27°44.9'N	14°25.0'W	ES	17.03.68
			CAPE VERDE BASIN				
Atlantic II	138	1976	30	10°36.0'N	17°52.0'W	ES	04.02.67
	139	2187	21	10°33.0'N	17°53.0'W	ES	04.02.67
	141	1796	38	10°30.0'N	17°51.5'W	ES	05.02.67
	142	1796	101	10°30.0'N	17°51.5'W	ES	05.02.67
	143	2095	18	10°35.0'N	17°44.0'W	ES	05.02.67
	144	2357	39	10°36.0'N	17°40.0'W	ES	05.02.67
	145	2185	25	10°36.0'N	17°49.0'W	ES	06.02.67

A closely related species appears to be *Nucula aegeensis* Forbes, (1844). Like many Forbes types, that of *N. aegeensis* has been lost, and although specimens named *N. aegeensis* exist and have been examined, eg. Jeffreys collections in the BM(NH) No. 85.11.5.560–4 and 85.11.5.567–570 and USNM, there is no certainty that these are in fact the species that Forbes described from off Crete. Indeed Jeffreys, (1879) is uncertain and states "Assuming this to be Forbes's species (although his description is too scanty to be satisfactory)."

Fig. 9 *Nuculoidea bushae*. Lateral and dorsal views of a shell from Station 87. (Scale = 1.0 mm).

Specimens of Jeffreys labelled *N. aegeensis* differ markedly in shape and fringe detail from *N. bushae*. Likewise Dall, (1886) also identified *N. aegeensis* from the Atlantic off Havana in 320 m and 823 m, off Morro Light 479 m and off St Vincent in 847 m regarding this as a geographical race of *Nuculoma tenuis* a view not supported by Jeffreys, (1879). There is certainly confusion, an easily accessible example is a comparison of the photograph in Abbott, (1974) of a West Atlantic specimen against a well-figured specimen in Locard, (1898). They are dissimilar in details of hinge and outline.

SHELL DESCRIPTION

The description by Verrill & Bush, (1898) is detailed and accurate.

Shell small, elongate-ovate, equivalve, inequilateral; semi-transparent, dentition often visible through shell, surface smooth, lustrous with fine concentric lines; umbos posterior to midline, orthogyrate, to slightly opisthogyrate; when posterior margin orientated vertically anterior dorsal margin is well above the horizontal; lunule often bordered by tiny perforations, escutcheon indistinct; teeth typical chevron-shape, number varying with size of specimen, 3 posterior and 4 anterior teeth in a specimen 1.64 mm in length and 6 posterior and 9 anterior teeth in a specimen 4.47 mm in length, ligament slightly oblique to moderately narrow hinge plate, does not extend ventral to anterior proximal teeth.

COMPARATIVE SHELL MEASUREMENTS OF *Nuculoidea bushae*

Dimension (mm)	No	Mean	SD	Max	Min
NORTH AMERICA BASIN					
Length	25	2.70	1.05	4.78	1.05
Width		1.23	0.479	2.28	0.53
Height		2.01	0.764	3.51	0.82
WEST EUROPEAN BASIN					
Length	23	2.05	0.75	4.11	0.86
Width		1.06	0.35	2.13	0.49
Height		1.64	0.55	3.26	0.60
BAY OF BISCAY					
Length	54	2.68	0.85	3.99	1.25
Width		1.44	0.51	2.36	0.68
Height		2.13	0.69	3.14	1.01
ANGOLA BASIN					
Length	55	2.23	0.95	5.91	0.73
Width		1.00	0.45	2.67	0.35
Height		1.72	0.72	4.38	0.59
GUYANA BASIN					
Length	28	1.18	0.46	2.54	0.76
Width		0.57	0.19	1.03	0.400
Height		0.92	0.33	1.82	0.61
CANARIES BASIN					
Length	5	3.24	0.99	3.85	1.47
Width		1.83	0.57	2.22	0.83
Height		2.65	0.818	3.17	1.21
CAPE VERDE BASIN					
Length	29	2.82	0.76	3.92	1.34
Width		1.46	0.44	2.15	0.73
Height		2.22	0.50	2.93	1.09

INTERNAL MORPHOLOGY

N. bushae differs from *Deminucula atacellana* in having a much more extensive foot with less pronounced papillae but with a marked heel. The 'byssal' gland is large. In *N. bushae* the adductor muscles are oval in cross-section and the anterior is slightly larger than the posterior. The 'quick' and 'catch' portions are approximately equal in size. The gill axis lies parallel to the postero-dorsal margin of the shell. The gill plates number 30 in a specimen 3.1 mm in length. The palps are relatively large compared with *D. atacellana* but do not extend beyond the limits of the foot. The palp ridges number 30 in a specimen ca. 2 mm in length. The palp proboscides, although highly contracted, appear to have the same relative proportions as in *D. atacellana*. The stomach differs from that of *D. atacellana* in being more slender and the hind gut is less extensive (Fig. 11). The maximum recorded diameter of ova from these samples is 140 µm. This is in contrast to Scheltema (1972) who recorded an egg diameter of 270 µm. We believe that this is because Scheltema (1972) had examined specimens of *N. similis* a species of very similar appearance. There is no evidence of seasonal reproduction and fully mature specimens were recorded in February, June, August and October.

DISTRIBUTION

Nuculoidea bushae occurs in the North America, Angola, Guinea, Guyana, Canaries, Cape Verde and West European Basin, the latter includes the Rockall Trough and the Bay of Biscay. Verrill & Bush, (1898) thought that *Nuculoidea bushae* to be closely related to the shallow water species *Nuculoma tenuis*. The shell is, however, much less oblique and more elongate than in the latter species, while the hinge plate of *N. bushae* is broader and the resilifer is more rounded, less oblique and does not extend ventral to the anterior teeth. Verrill & Bush, (1898) collected *N. bushae* from four U.S. Fisheries Commission stations in the North American Basin between Lat. 40°00.0'N. Long. 71°14'30"W, and Lat. 37°8'N, Long. 74°33'W., in 287–812 m but, until now, the species has not been recorded from other regions of the Atlantic.
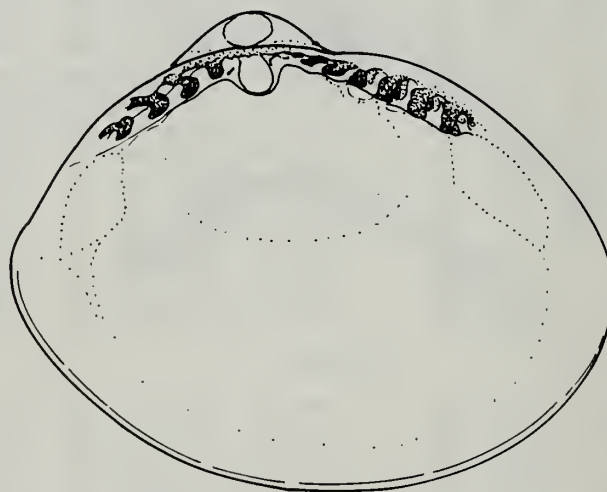

Fig. 10 *Nuculoidea bushae*. Internal view of left valve from Station 314. (Scale = 1.0 mm).
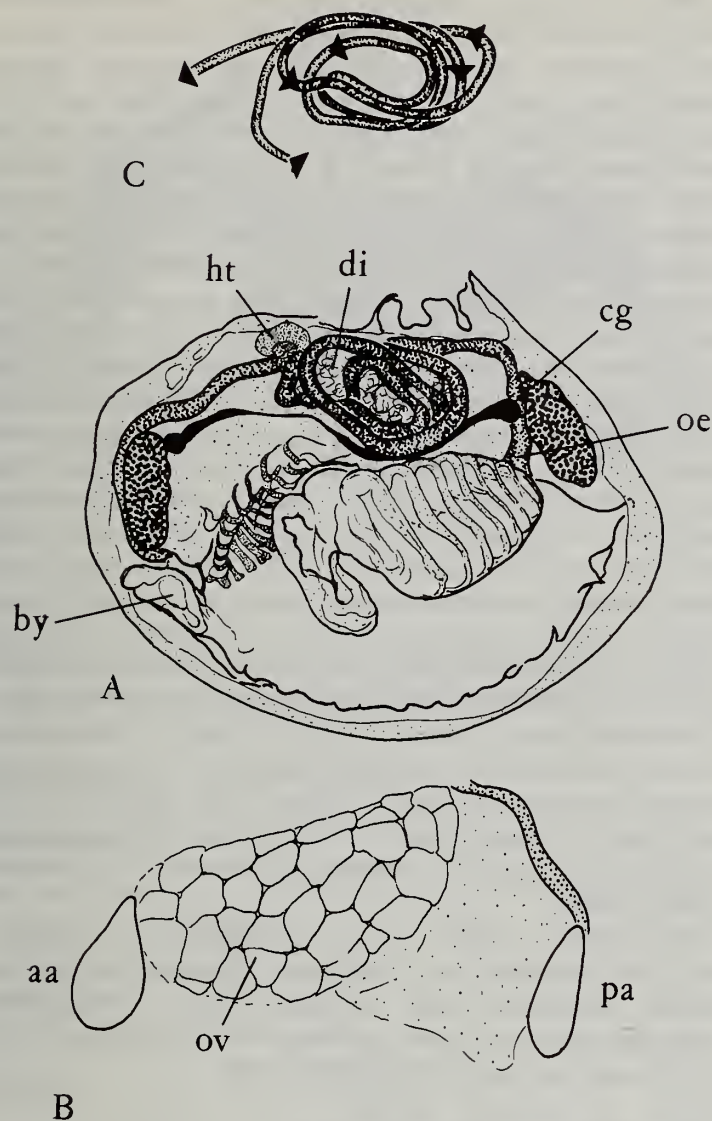
Fig. 11 *Nuculoidea bushae*. A. Semidiagrammatic view from the right side of the body organs; B. Lateral view of part of body from the left side to show the position of the ovary in a mature specimen; C. Course of hind gut as seen from the right side. (Scale = 1.0 mm; for key to abbreviations see p.63).

Nuculoidea pernambucensis (Smith 1885)

Figs 12–14

TYPE LOCALITY: Challenger Sta. 120, Lat. 08°37'00"S, Long. 34°28'00"W, 675 fms.

TYPE SPECIMENS: Syntypes, 5 valves, BM(NH) reg.no. 1887.2.9.2910–11. (Examined by PR). (Note: Two specimens from Knorr, Sta. 293, 08°58.0'N, 54°04.3'W, 1518 m lodged in BM(NH) No. 1990012).

Nucula pernambucensis Smith, 1885, p. 227, pl. 18, Figs 10–10a.
Nucula cymella Dall, 1886, p. 246; 1889, p. 42; 1890, p. 258, pl. 13, Fig. 1; 1903, p. 42; Johnson, 1934, p. 16; Clarke, 1962, p. 48; Knudsen 1970, p. 220.
Nucula turnerae Clarke, 1961, p. 367, 368; pl. 2, Figs 2, 3; 1962, p. 49.

DEPTH RANGE: 587–2976 metres.

Nucula cymella Dall, (1890) was synonymized with *Nuculoidea pernambucensis* by James, (1972). Clarke, (1960) noted that *Nucula turnerae* from the Argentine Basin was similar to *Nuculoidea pernambucensis* and that it was possibly

a juvenile specimen of the latter species. Verrill & Bush, (1898) also noted *Nuculoidea bushae* resembled both *Nuculoidea pernambucensis* and *Nuculoma tenuis*. *N. pernambucensis* appears to be closely related and probably congeneric with *Nucula* sp. A described by James, (1972) from the Gulf of Mexico.

MATERIAL

Cruise	Sta	Depth (m)	No	Lat	Long	Gear	Date
				GUYANA BASIN			
Knorr	293	1518	23	08°58.0'N	54°04.3'W	ES	27.02.72
	299	2076	3	07°55.1'N	55°42.0'W	ES	29.02.72
				BRAZIL BASIN			
Atlantis II	167	975	4	07°58.0'S	34°17.0'W	ES	20.02.67
	169	587	12	08°03.0'S	34°23.0'W	ES	21.01.67

SHELL DESCRIPTION

The original description by Smith, (1885) is not very detailed.

Shell broadly ovate, somewhat triangular, equivalve, inequilateral, transluscent, with dentition often visible through shell, strong concentric ridges; umbos posterior to the midline, orthogyrate; when postero-dorsal margin orientated vertically antero-dorsal margin well above horizontal; lunule often bordered by tiny perforations, escutcheon indistinct; hinge-teeth, small, pustular, 3 posterior and 4 anterior teeth in specimen of 1.97 mm in length, and 9 posterior and 11 anterior teeth in specimen 5.70 mm in length, ligament perpendicular to very broad hinge plate, does not extend ventral to anterior proximal teeth.

COMPARATIVE SHELL MEASUREMENTS OF *Nuculoidea pernambucensis*

Dimension (mm)	No	Mean	SD	Max	Min
		GUYANA BASIN			
Length	19	3.69	0.85	5.06	1.97
Width		2.00	0.54	3.02	0.97
Height		2.99	0.69	4.06	1.56
		BRAZIL BASIN			
Length	9	3.92	0.73	5.70	3.25
Width		2.17	0.57	3.54	1.64
Height		3.26	0.63	4.73	2.60

N. pernambucensis appears to be unique among extant nuculids in possessing an extremely broad hinge plate with narrow obtuse and somewhat pustulate teeth (Fig. 12). This feature is fairly common among Palaeozoic species, for example species of *Tancrediopsis* Beushausen (McAlester, 1963; Bradshaw, 1970) and *Nuculoidea* Williams & Breger (Vokes, 1949). This type of hinge is also present in an unusual nuculoid *Tironucula jugata* from the Lower Ordovician of Spitzbergen (Morris & Fortey, 1976). This latter species originally placed in a family Praenuculidae (McAlester, 1969) was later regarded by Morris & Fortey, (1976), on the basis of
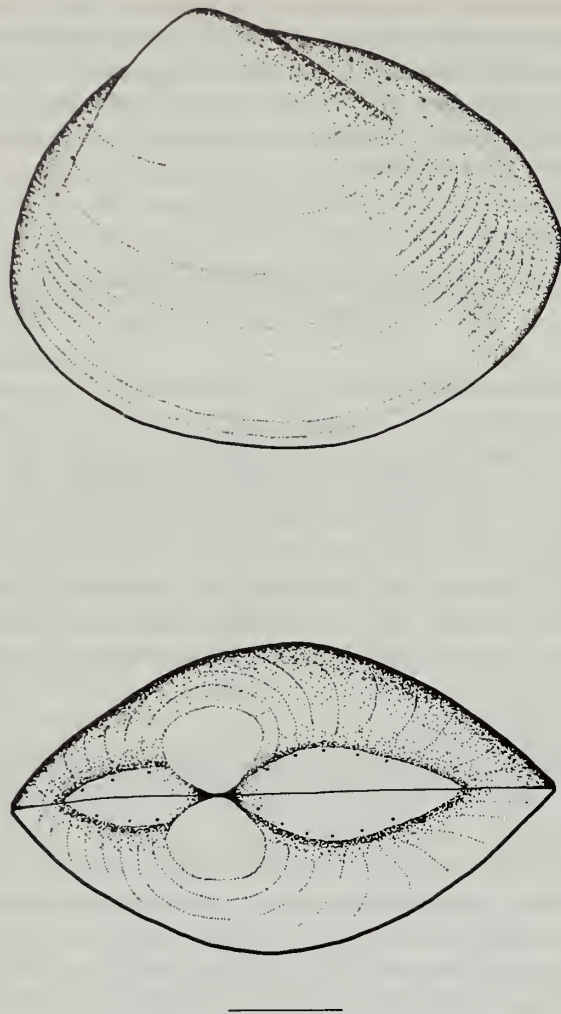
Fig. 12 *Nuculoidea pernambucensis*. Lateral and dorsal views of a shell from Station 293. (Scale = 1.0 mm).

its hinge morphology, as intermediate between taxodont and actinodont forms. Actinodont dentition is probably the more primitive and gave rise to the taxodont condition. Allen & Sanders, (1973) point out that the lack of taxodont teeth *per se* can no longer be used as the prime criterion for excluding fossil bivalves from the Nuculoidea. *N. pernambucensis* also resembles the Silurian fossil *Nuculoidea pinguis pinguis* (Soot-Ryen, 1964); *N.p. pinguis* together with members of the primitive nuculoid family Ctenodontidae, are thought by Soot-Ryen, (1964) to have lived in a deep-sea environment. This is based on the fact that they lived in muddy sediments so tranquil that valves did not separate after the animal's death.

INTERNAL MORPHOLOGY
The adductor muscles are oval, the anterior being slightly larger than the posterior. The 'quick' and 'catch' portions are approximately equal in size. The gill axis lies parallel to the posterior dorsal margin of the shell and gill plates number 20 in a specimen 3.9 mm in length. The palps are relatively longer than those of *D. atacellana* and palp ridges number 40 in a specimen 4 mm in length. The 'byssal' gland is large.

DISTRIBUTION
Because only dead valves had been collected from abyssal depths Knudsen, (1970) did not regard *Nuculoidea pernambucensis* as truly abyssal, and James, (1972) on the basis of collections from the Gulf of Mexico, also supported this view. The results here confirm that it occurs at abyssal depths at least in the Guyana Basin.

HMS 'Challenger' originally collected *N. pernambucensis* off Pernambuco (Recife) on the slope of the Brazil Basin. *Nucula cymella* was recorded from the Yucatan Straits, Florida Strait, south of Cuba, east of Tobago and north of Ceara, Brazil (Dall, 1890) and *N. turnerae* was collected in the Argentine Basin at 'Vema' Sta. 12 (Clarke, 1961). James, (1972) collected *N. pernambucensis* in the north east and the north west of the Gulf of Mexico at depths of 732–1683 m but living specimens were only taken in depths of 1000–1494 m.

Since specimens are found at upper slope depths it is possible that *N. pernambucensis* may have evolved following a downward migration of an adjacent shelf species of the tropical shelf of South America and/or the Gulf of Mexico. Such a theory may explain why this, unlike other deep-water species, is large and has unusually strong concentric ridges and why the hinge plate is heavily calcified. Tropical molluscs tend to be more heavily calcified (Vermeij, 1978; Nicol, 1964; 1965, 1966 and 1967) and Moore, (1977) lists a number of heavily calcified endemic tropical nuculid species with strong concentric ridges. Conversely, reduced calcification is characteristic of deep-water species (Nicol, 1967) and is related to low temperatures and to high pressure (Grause, 1974). Thus, *N. pernambucensis* is unusual in this respect. Unfortunately no living shallow-water species similar to *N. pernambucensis* occurs in the tropical western Atlantic today (Moore, 1977), nor is there a similar species in the Holocene formations of Surinam even though a number of nuculids are present (Altena, 1968).

N. pernambucensis has the second-largest size of ovum of the species recorded here. The largest diameter recorded was 204 μm, sufficiently large to predict direct development rather than the more-typical lecithotrophic development with a free-swimming stage (Ockelmann, 1965).

Nuculoma perforata (new species)

Figs 17–19

TYPE LOCALITY: Atlantis II. Sta. 236, 36°27.0′S, 53°31.0′W, 518 m.

TYPE SPECIMEN: Holotype BM(NH) No. 1990008 from type locality; paratypes at present lodged at Woods Hole Oceanographic Institution (10 specimens in lot).
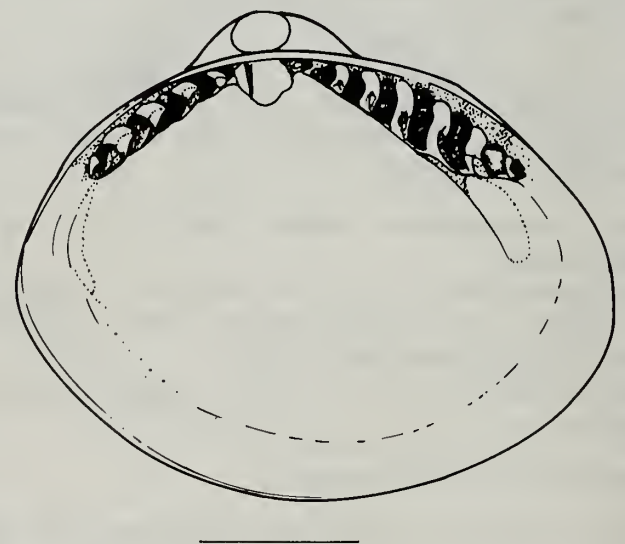

Fig. 13 *Nuculoidea pernambucensis*. Internal view of the left valve of a shell from Station 293. (Scale = 1.0 mm).
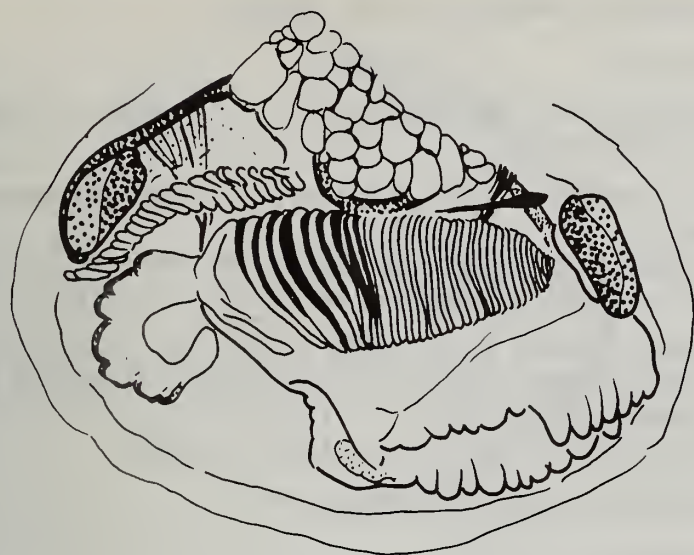
Fig. 14 *Nuculoidea pernambucensis*. Semidiagrammatic view from the right side of the body organs. (Scale = 1.0 mm). See figures 5 & 15 for identification of the parts.

DEPTH RANGE: 518–2323 metres.

MATERIAL

Cruise	Sta	Depth No (m)		Lat	Long	Gear	Date
			ARGENTINE BASIN				
Atlantis II	236	518	15	36°27.0'S	53°31.0'W	ES	11.03.71
	237	1011	7	36°32.6'S	53°23.0'W	ES	11.03.71
	239	1679	37	36°49.0'S	53°15.4'W	ES	11.03.71
	240	2323	11	36°53.4'S	53°10.2'W	ES	12.03.71
	262	2480	1	36°15.1'S	52°1.79'W	ES	27.03.71
	264	2048	1	36°12.7'S	52°42.7'W	AD	28.03.71

SHELL DESCRIPTION

Shell small, elongate-ovate, equivalve, inequilateral; dentition usually visible through the dorsal part of the shell, smooth with fine concentric lines; umbo posterior to midline, opisthogyrate; when posterior margin orientated vertically, anterior dorsal margin is above horizontal; lunule usually bordered by tiny perforations, escutcheon, indistinct; resilifer oblique to narrow hinge plate, except in small specimens (<2 mm) extends ventral to anterior proximal teeth; hinge teeth chevron-shaped, the number varies with size, 3 posterior and 4 anterior teeth, in a specimen 1.6 mm in length and 4 posterior and 8 anterior teeth, in a specimen 4.7 mm in length.

SHELL MEASUREMENTS OF *Nuculoma perforata*

Dimension (mm)	No	Mean	SD	Max	Min
		ARGENTINE BASIN			
Length	20	2.95	1.7	9.04	1.42
Width		1.46	0.68	3.67	0.79
Height		2.24	1.27	6.54	1.07
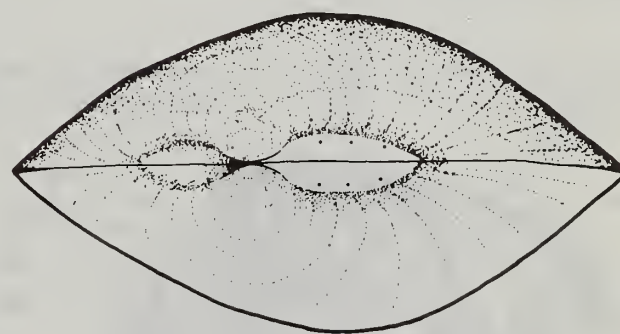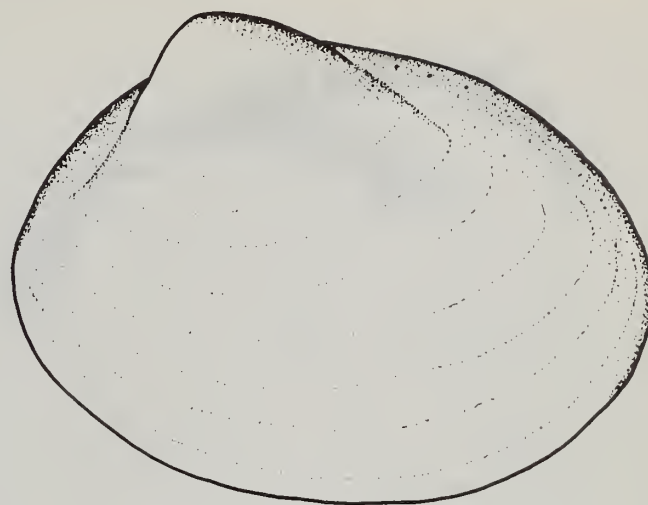
Fig. 15 *Nuculoma perforata*. Lateral and dorsal views of a shell from Station 239. (Scale = 1.0 mm).

INTERNAL MORPHOLOGY

The adductor muscles are oval in cross section the anterior being larger than the posterior (not obvious in Fig. 17 because of angle of view). The 'quick' and 'catch' portions are approximately equal. The gill axes lie parallel to the posterodorsal margin of the shell. Gill plates number 18 in a specimen 3.7 mm in length. The palps are slightly smaller than those of *N. subovata* and do not extend to the posterior limit of the foot. There are also relatively fewer palp ridges (15 in a specimen 3.7 mm in length). The palp proboscides are typical but the 'byssal' gland is smaller than that of *D. atacellana*. This species has an exceptionally large stomach (Fig. 17).

DISTRIBUTION

Nuculoma perforata is restricted to the Argentine Basin. It appears to be closely related to the much-larger species *Nucula puelcha* d'Orbigny, 1842 from the adjacent continental shelf (Schenck, 1939). *Nucula puelcha* is similar to *Nuculoma tenuis* and should now be classified as a member of the genus *Nuculoma*. *N. puelcha* is present in WHOI collections from shallow-water stations adjacent to the Argentine Basin and we have considered the possibility that *N. perforata* may be young slow-growing specimens of *Nuculoma puelcha*, close to the limit of their bathymetric range. Although no mature specimens of *Nuculoma perforata* are present in the samples they differ in the configuration of the hindgut (Fig. 18) and furthermore they were more abundant at

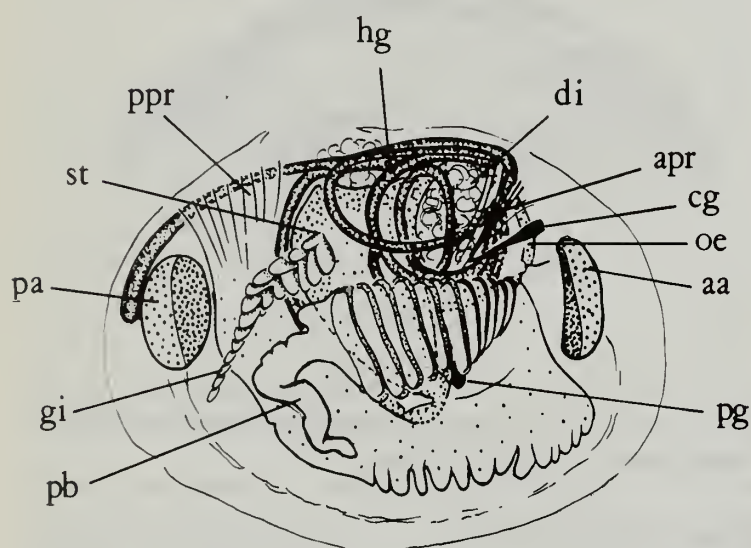Fig. 16 *Nuculoma perforata*. Internal view of left valve of shell from Station 236. (Scale = 1.0 mm).

Fig. 17 *Nuculoma perforata*. Semidiagrammatic view of right side of the body to show arrangement of organs. (Scale = 1.0 mm; for key to abbreviations see p.63).
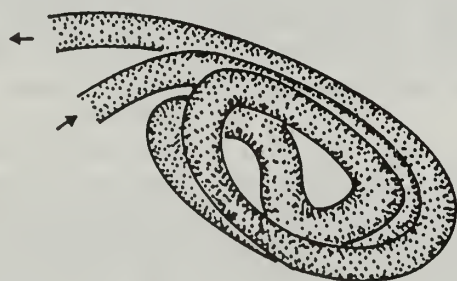

Fig. 18 *Nuculoma perforata*. The course of the hind gut as seen from the right side.

1670 m than at 507 m. We believe *N. perforata* to be a separate but closely related species to *N. puelcha*.

The species has some similarity with specimens dredged from relatively shallow water off the coast of Guyana (exact locality unknown) and named *Nucula surinamensis* by Altena, (1968).

Nuculoma granulosa (Verrill, 1884)

Figs 19–22

TYPE LOCALITY: Fish Hawk Sta. 892, Lat. 39°46′00″N, Long. 71°10′00″W, 891 m.

TYPE SPECIMEN: Holotype USNM No. 52561. (Examined JAA).
  (Note: 5 specimens from Sarsia, Sta. S63, 46°17.5′N, 04°45.2′W, 1336 m lodged in BM(NH) No. 1990015).

Nucula granulosa Verrill, 1884, p. 280; Dall, 1889, p. 42; Verrill & Bush, 1898, p. 853, pl. 81, Fig. 2, pl. 88, Fig. 8; Johnson, 1934, p. 15.
Nucula cortica Grassle, 1977, p. 618; 1978, p. 42.

DEPTH RANGE: 811–2178 metres.

MATERIAL

Cruise	Sta	Depth (m)	No	Lat	Long	Gear	Date
			NORTH AMERICA BASIN				
Atlantis	F1	1500	33	39°47.0′N	70°45.0′W	AD	24.05.61
Atlantis II	73	1470	1143	39°46.5′N	70°43.3′W	ES	25.08.64
Chain	87	1102	844	39°48.7′N	70°40.8′W	ES	06.07.65
	103	2022	6	39°43.6′N	70°37.4′W	ES	04.05.66
	105	530	232	39°56.6′N	70°03.6′W	ES	05.05.66
Atlantis II	128	1254	5	39°46.5′N	70°45.2′W	ES	16.12.66
	131	2178	1	39°38.5′N	70°36.5′W	ES	18.12.66
Chain	207	811	161	39°51.0′N	70°56.4′W	ES	21.02.69
	209	1693	887	39°46.0′N	70°51.5′W	ES	22.02.69
	210	2064	6	39°43.2′N	70°49.5′W	ES	23.02.69
			WEST EUROPEAN BASIN				
Sarsia	S63	1336	31	46°17.5′N	04°45.2′W	ES	24.07.67
Challenger	ES20	1271	48	56°46.0′N	09°15.0′W	ES	23.09.73

Verrill, (1884) originally described the species as occurring in the North America Basin at U.S. Fisheries Commission stations 892, 1880, 1883 and 2072. This was later updated by Verrill & Bush, (1898) to include six stations between Lat. 39°43′45″N, Long. 70′7 W. and Lat. 36°47′N, Long. 73°9′30″W, in 2086–3340 m (station numbers were not given). Dall, (1889) describes the species as having a latitudinal range off the east coast of N. America from Georges Bank in the North to Cape Lookout in the South. This study extends its range to the Bay of Biscay and the Rockall Trough.

SHELL DESCRIPTION
The original description by Verrill, (1884) is not very detailed.
  Shell very small, broad-ovate, equivalve, inequilateral, opaque surface smooth with fine concentric lines; umbo posterior to midline, opisthogyrate; when posterior margin orientated vertically, anterior dorsal margin is below horizontal; lunule bordered by angular ridge, escutcheon, indistinct; hinge teeth chevron-shaped, the number varying with size, 2 posterior and 3 anterior teeth in a specimen 0.94 mm in length, and 4 posterior and 6 anterior teeth in a specimen 1.98 mm in length; ligament large, perpendicular to relatively broad hinge plate, does not extend ventral to the anterior proximal teeth. Although the external shell morphology is somewhat variable, it must be regarded as a single species.
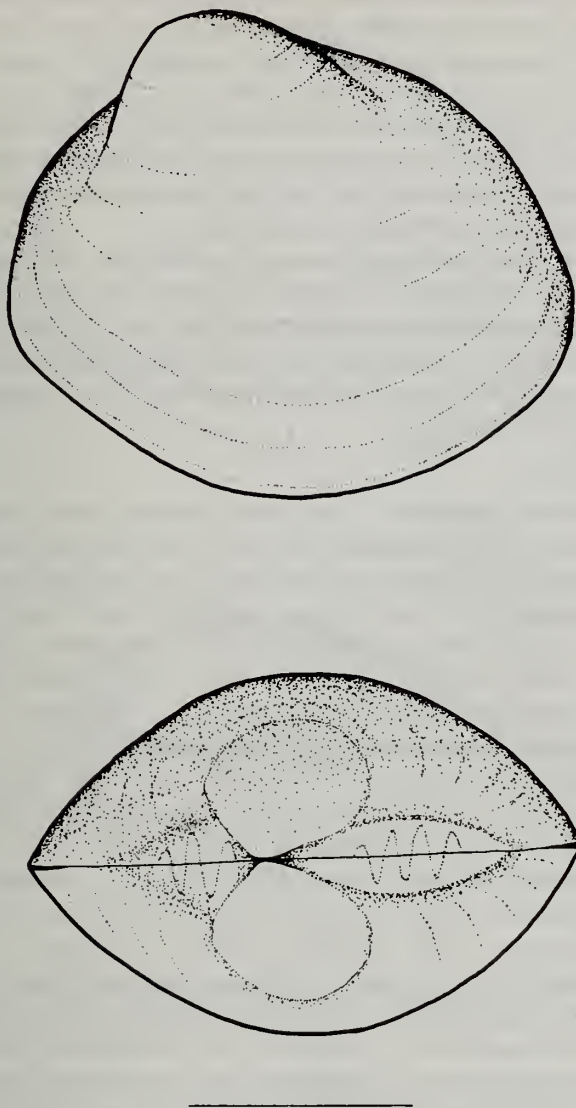
Fig. 19 *Nuculoma granulosa*. Lateral and dorsal views of a shell from Station 73. (Scale = 1.0 mm).

COMPARATIVE SHELL MEASUREMENTS OF *Nuculoma granulosa*

		NORTH AMERICA BASIN			
Length	22	2.05	0.28	2.45	1.39
Width		1.18	0.45	1.75	0.85
Height		1.81	0.27	2.26	1.22
		BAY OF BISCAY			
Length	10	1.76	0.16	1.93	1.42
Width		1.06	0.12	1.21	0.83
Height		1.54	0.14	1.69	1.21

INTERNAL MORPHOLOGY

The adductor muscles are oval and the anterior is larger than the posterior. The 'quick' and 'catch' portions are approximately equal. The gill axis lies parallel to posterior margin of the shell and the gill plates number 14 in a specimen ca. 2 mm in length. The palps do not extend to the posterior limit of the foot. The palp ridges number 16 in a specimen ca. 2 mm in length. The foot has a similar orientation and relative size to that of *Deminucula atacellana*, but the 'byssal' gland is narrower.

The hind gut configuration is also similar to that of *D. atacellana*. The maximum recorded diameter of the egg is
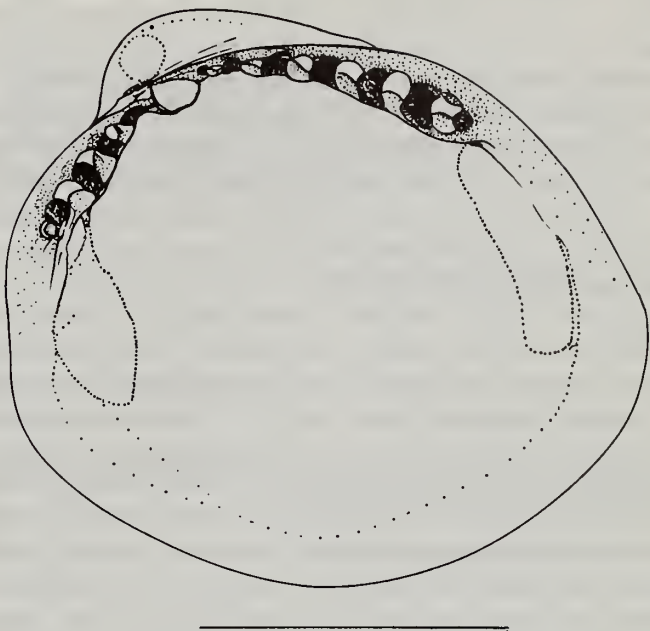
Fig. 20 *Nuculoma granulosa*. Internal view of left valve of shell from Station 563. (Scale = 1.0 mm).
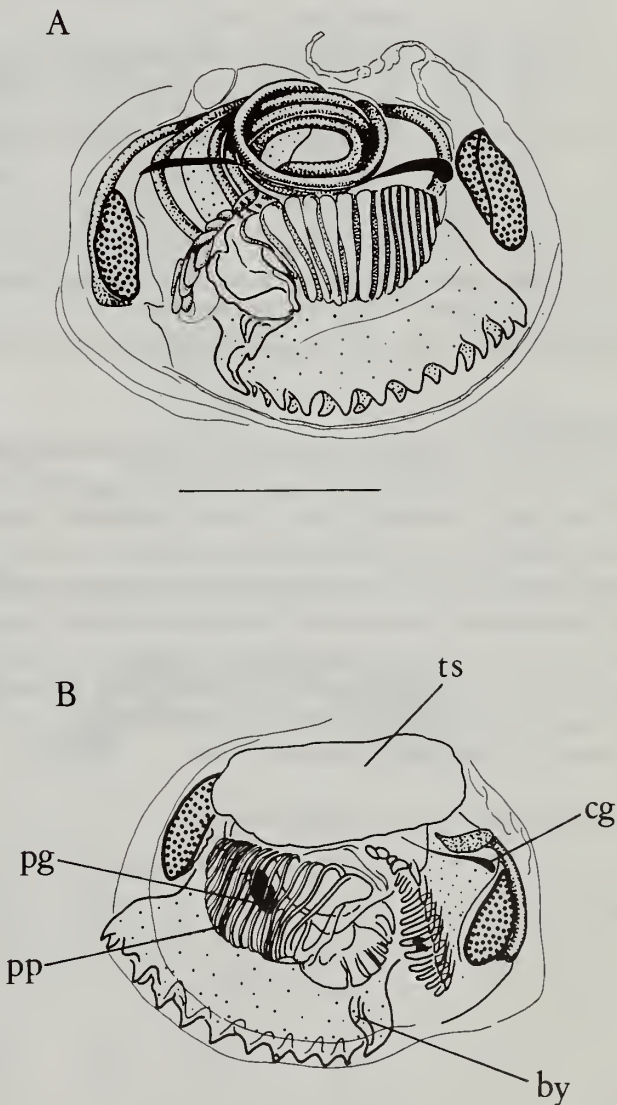
Fig. 21 *Nuculoma granulosa*. Semidiagrammatic views of A, right and B, left side of body of different specimens to show arrangement of body organs. (Scale = 1.0 mm; see Fig. 19 for identification of parts and for key to abbreviations see p.63).

120 µm (Scheltema, 1972) with approximately 220 eggs in a specimen 2.2 mm total length.

DISTRIBUTION

It is an upper slope stenobathic species. It is closely related to *Nucula corticata* Möller, 1842 (Sowerby, 1871) a Greenland shallow-water species suggesting, as in the case of *Nuculoma similis* (see p.81 *et seq.*), a high latitude shallow-water derivation.

Nuculoma similis (new species)

Figs 23–25

TYPE LOCALITY: Chain Sta. 96, Lat. 39°55.2′N, Long. 70°39.5′W, 498 metres.

TYPE SPECIMEN: Holotype: BM(NH) No. 199005; Paratypes No. 1990006 (5 specimens in lot).

DEPTH RANGE: 498–2064 metres.

MATERIAL

Cruise	Sta	Depth (m)	No	Lat	Long	Gear	Date
				NORTH AMERICA BASIN			
Atlantis	E3	823	37	39°59.5′N	70°35.0′W	AD	25.05.61
Atlantis II	73	1470	126	39°46.5′N	70°43.3′W	ET	25.08.64
Chain	87	1102	270	39°48.7′N	70°40.8′W	ET	06.07.65
	88	478	34	39°54.1′N	70°37.0′W	ET	06.07.65
	96	498	86	39°55.2′N	70°39.5′W	ET	27.04.66
	103	2022	2	39°43.6′N	70°37.4′W	ET	04.05.66
Atlantis II	128	1254	27	39°46.5′N	70°45.2′W	ES	16.12.66
Chain	207	811	1348	39°46.5′N	70°56.4′W	ES	21.02.69
	209	1693	200	39°46.0′N	70°51.5′W	ES	22.02.69
	210	2064	1	39°43.2′N	70°49.5′W	ES	23.02.69

SHELL DESCRIPTION

Shell subtriangular, oblique, ventricose, equivalve, inequilateral; surface lustrous with fine concentric lines; umbos posterior to midline, opisthogyrate; when posterior margin orientated vertically, the antero-dorsal margin is below horizontal; indistinct lunule, chordate shaped escutcheon; hinge teeth chevron-shaped, the number varying with size, 1 posterior and 3 anterior teeth in a specimen 1.6 mm in length, and 3 posterior and 6 anterior teeth in a specimen 2.6 mm in length; ligament oblique to narrow hinge plate, extends slightly ventral to anterior proximal teeth.

SHELL MEASUREMENTS OF *Nuculoma similis*

Dimension (mm)	No	Mean	SD	Max	Min
		NORTH AMERICA BASIN			
Length	71	1.97	0.420	3.03	1.19
Width		1.18	0.255	2.87	0.73
Height		1.62	0.351	1.61	1.01

INTERNAL MORPHOLOGY

The adductor muscles are approximately equal in size, more or less oval in shape. The anterior part of the gill axis lies

parallel to the dorsal margin of the shell but posteriorly it curves to lie parallel to the posterior margin. The gill plates number 15 in a specimen ca. 3 mm in length. The palps are small with 16 palp ridges in a specimen of ca. 3 mm in length. In preserved specimens the foot is laterally compressed and the 'byssal' gland is extremely small. The stomach has an unusually small style sac. The hind gut configuration is not as complex as that of *Deminucula atacellana*.

N. similis has the largest ovum recorded for any species described in this paper (maximum diameter 244 µm). Scheltema, (1972) recorded a maximum egg size of 270 µm for *N. subovata* which was almost certainly a misidentification for *N. similis* (see p. 73). There can be little doubt that this species has direct development.

DISTRIBUTION

This species is restricted to the North America Basin. In view of the intensity of past sampling in this Basin, it is curious that it has never been described previously, particularly as it is more abundant and has a greater vertical depth range than that of *Nuculoidea subovata* (p. 73). *Nuculoma similis* appears to be closely related to the Arctic shallow-water species *Nuculoma bellotii* (Fig. 26) (cf. 2 specimens from 181 m off Baffin Island BM(NH) No. 1990014).

The taxonomic status of *N. bellotii* has been disputed. Three Arctic species, *Nucula inflata* Hancock, 1846, *Nucula expansa* Reeve, 1855, and *Nucula bellotii* Adams, 1856, have been regarded as being conspecific with, or varieties of, *Nuculoma tenuis* (Gould, 1870; Whiteaves, 1901; Soot-Ryen, 1932; Filatova, 1948; Thorsen, 1951; Ockelmann, 1958; MacGinitie, 1959). Schenck, (1939) regarded the three Arctic species as synonymous and because the names *Nucula inflata* and *Nucula expansa* are homonyms the first available name is *Nucula bellotii*. Schenck accepted the subgenus *Ennucula* (Iredale) and named the species *Nucula (Ennucula) bellotii*. Schenck, (1939) also synonymized *N. bellotii* with the North
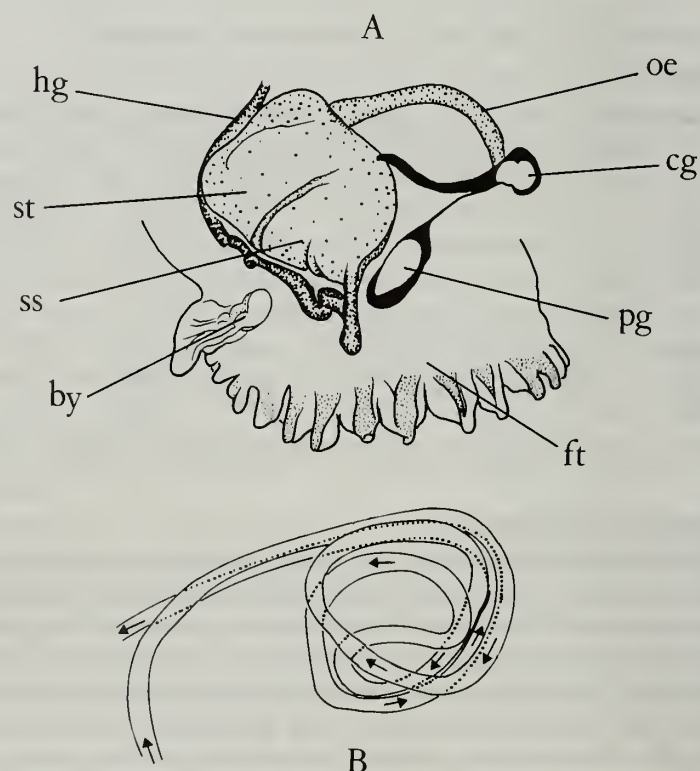

Fig. 22 *Nuculoma granulosa*. A. Detail of stomach and anterior part of nervous system and B. The course of the hind gut as seen from the right side. (For key to abbreviations see p.63).
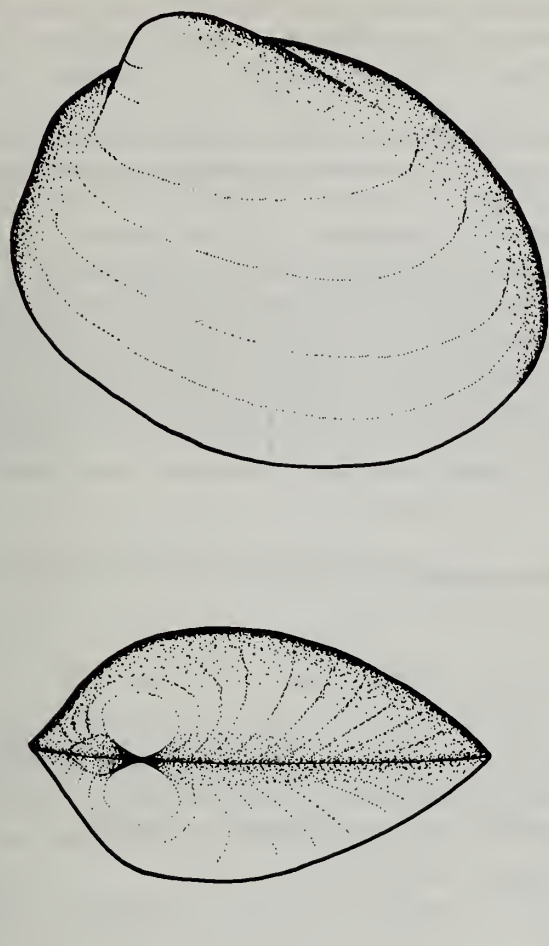
Fig. 23 *Nuculoma similis.* Lateral and dorsal views of shell from Station 207. (Scale = 1.0 mm).

Pacific species *N. quirca* Dall. Filatova, (1948) reports that an *inflata-expansa* complex (*N. bellotii*) as occurring in deep waters of the Barents and Bering Seas, while Lubinsky, (1972) also reported that specimens collected by Krause, (1885) from the Bering Straits and by MacGinity, (1959) from Point Barrow, and identified as *N. tenuis* Mont., *N. inflata* Hancock and *N. expansa* Reeve, were *N. bellotii*. Lubinsky's study indicates that *N. bellotii* occurs throughout the Canadian Arctic and she regards it as a circumpolar, panarctic species and separate from *N. tenuis*, however, she inferred that *N. bellotii* might be a subspecies of *N. tenuis*, although from comparisons of *N. tenuis* from Scottish waters, we doubt that. Both are species of the genus *Nuculoma*.

Bernard, (1979) collected specimens of *Nuculoma bellotii* from 132 stations throughout the Beaufort Sea. Abundant in depths <200 m it was also taken from depths down to 2560 m, showing that although *N. bellotii* is large (up to 20 mm in length) it is capable of deep-water existence. Recently Farrow *et al.*, (1984) recorded *N. bellotii* from the Baffin Island fjords McBeth and Cambridge. These latter specimens were made available for comparative study (see Table below). Wagner, (1968) regarded fossil *Nuculoma bellotii*, collected by Bell, (1879) in the Hudson Bay area as part of the faunal assemblage of the Tyrrel Sea. Due to uplift much of this sea which reached its maximum extent between 5000 and 6000BC, disappeared with only remnants such as Hudson Bay and James Bay now remaining.

Nuculoma similis and *N. bellotii* share similar external shell features (eg. The characteristic 'pouting' of the anterior dorsal margin). As is usually the case with deep-sea species, specimens of *Nuculoma similis* are by far the smaller. The

Table below lists the ratios of the height/length and width/length of *N. bellotii* taken from various localities (Lubinsky, 1972) compared with those of *Nuculoma similis*. Those of *Nuculoma similis* fall well within the range of *N. bellotii*. As in *Nuculoma similis*, the h/l and w/l ratios of *N. bellotii* are normally distributed (Lubinsky, 1972) and it is highly probable that *N. bellotii* and that inflated specimens (= *Nucula inflata* Hancock) and elongate, narrow ones (= *Nucula expansa* Reeve) are extreme variants of a unimodal population of a single species. If *Nuculoma similis* is a sibling species of *N. bellotii* it would help to explain why the former species only occurs in the North America Basin. Shallow-water specimens of *N. bellotii* from Baffin Bay and the Labrador Sea would presumably have been the origin of a sibling population adapted to deep water and early isolated in the North America Basin. That *N. bellotii* is not present on the New England shelf is probably due to it being a cold-water stenothermic species. The absence of *Nuculoma similis* from other Basins is probably related to the fact that it has direct development. Note that *N. bellotii* also has direct development, but from a much smaller egg (maximum diameter 163 μm). Stenothermy would also tend to isolate it to the deep sea and prevent it crossing boundary ridge systems. Both species are absent from the Norwegian Basin (Bouchet & Warén, 1979) which would suggest their centre of origin to be in the North Pacific.

SHELL MEASUREMENTS OF *Nuculoma bellotii* (from Lubinsky, 1972)

Species	Location	No	Length (mm)	h/l	w/l
Nuculoma bellotii	Foxe Basin	40	8–17	0.73–0.85	0.49–0.65
" " "	Hudson Bay	80	6–12	0.70–0.90	0.49–0.67
" " "	Ponds Inlet	10	7–14	0.77–0.82	0.47–0.67
" " "	Wellington Ch & Frobisher Bay	14	10–16	0.78–0.86	0.49–0.68
" " "	Labrador	16	10–16	0.79–0.90	0.54–0.64
Nuculoma similis	N. America Basin	71	1.19–3.03	0.79–0.89	0.54–0.65

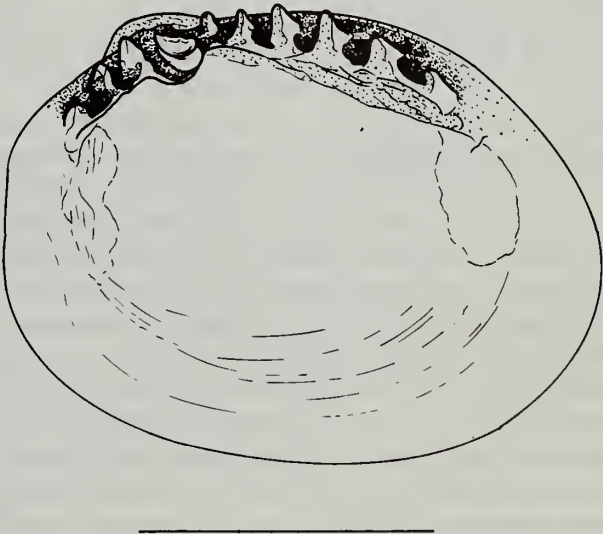Other Atlantic Arctic species to which *Nucula granulosa*

Fig. 24 *Nuculoma similis.* Internal view of left valve of shell from Station 96. (Scale = 1.0 mm).
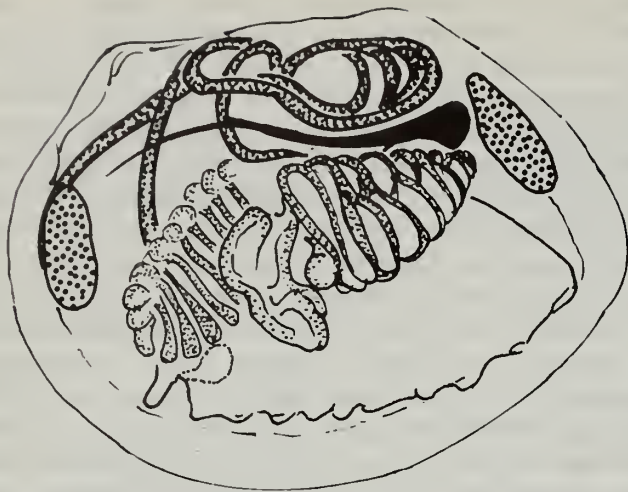
Fig. 25 *Nuculoma similis*. Semidiagrammatic view of right side of body to show arrangements of organs. (Scale = 1.0 mm; see Fig. 19 for identification of parts).
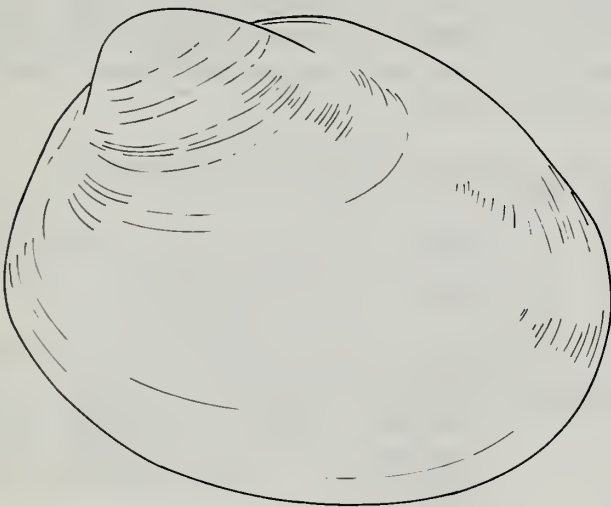

Fig. 26 *Nuculoma bellotii*. Lateral view of right valve of shell from Hudson Bay. (Scale = 1.0 mm).

and *N. similis* have possible similarity are *N. corticata* and *N. delphinodonta*. *N. delphinodonta* has a predominantly arctic shelf distribution, but off the Eastern Seaboard of the USA it extends south from Labrador to Maryland (Ockelmann, 1958; Abbott, 1974). Thus, its distribution is adjacent to that of *N. similis*. Furthermore, it has a large egg which has direct development, eggs being brooded in a secretion of the pallial gland attached to the posterior part of the shell. Although *N. similis* has a large egg, we have no evidence to indicate that brooding occurs. Although similar in shape and size, *N. delphinodonta* a short, stout species with a truncate posterior margin, can be distinguished by its coarse concentric growth lines, and a slight dorsal carination. Other differences include an average anterior to posterior hinge teeth ratio of 3:7 as compared with 3:6 for *N. similis*; the hinge teeth of *N. similis* are stouter and the hinge plates are broader particularly the anterior above which the antero-dorsal margin is more raised with greater curvature. Nevertheless, the two species appear to be closely related.

In comparison with *N. granulosa*, there is less similarity. *N. granulosa* is a much shorter species with fewer anterior hinge

teeth and a shell outline that is significantly different from *N. delphinodonta*. *N. granulosa* has eggs of much smaller size, and almost certainly has a short, non-feeding, planktonic larva.

Comparison with *N. corticata* is much more difficult, simply because so little is known of this species. It was described as a Greenland species in Möller, (1842) and further described and illustrated by Sowerby, (1871) in Volume 18 of Reeve's *Conchologia Iconica*. There is little mention of it in the literature on the molluscan fauna of Greenland and Eastern Canada since then except that Soot-Ryan, (1966) records three specimens from the Michael Sars Expedition at 1100 m previously recorded as *N. tenuis* by Greig, (1920). Posteriorly the shell is rounded and not truncate as in *N. similis* and *N. granulosa*. Indeed, in outline *N. corticata* would appear to be similar to *N. tenuis expansa*.

Nuculoma elongata (new species)

Figs 27–28

TYPE LOCALITY: Knorr Sta. 297, Lat. 7°45.3′, Long. 54°24′W.

TYPE SPECIMENS: Holotype: BM(NH) No. 1990007 from type locality; paratypes at present lodged at Woods Hole Oceanographic Institution (2 specimens in lot).

DEPTH RANGE: 508–523 metres.

MATERIAL

Cruise	Sta	Depth (m)	No	Lat	Long	Gear	Date
				GUYANA BASIN			
Knorr	297	508–523	8	07°45.3′N	54°24.0′W	ES	28.02.72

SHELL DESCRIPTION
Shell very small, elongate-ovate, equivalve, inequilateral; surface smooth with fine concentric and radial striations, umbo posterior to midline, orthogyrate; when postero-dorsal margin orientated vertically antero-dorsal line is above the horizontal, posterior margin, dorsal to midline with faint concavity, lunule, bordered by tiny indistinct perforations, escutcheon, indistinct; ligament oblique to narrow hinge plate, not extending ventral to the anterior proximal teeth; 3 posterior and 4 anterior teeth in a specimen 2.1 mm in length.

SHELL MEASUREMENTS OF *Nuculoma elongata*

Dimension (mm)	No	Mean	SD	Max	Min
		GUYANA BASIN			
Length	5	1.75	0.24	2.01	1.47
Width		0.84	0.08	0.93	0.73
Height		1.30	0.15	1.47	1.11

INTERNAL MORPHOLOGY
The adductor muscles are oval in shape and approximately equal in size. The 'quick' and 'catch' portions are also

approximately equal in size. The gill axis lies parallel to the posterior margin. There are eight gill plates and twelve palp ridges in a specimen ca. 2 mm in length. The foot is large and has a similar orientation to that of *Nuculoidea* and when retracted extends anterior to the anterior adductor muscle. The 'byssal' gland is large.

REMARKS

All specimens were collected from one station in the Guyana Basin from the upper slope in a depth of 508–523 m. A number of the larger specimens had mature gonads, indicating that they were not the young of a larger species. There is no species of similar shell shape and characteristics in adjacent waters.

Brevinucula verrilli (Dall, 1886)

Figs 29–32

TYPE LOCALITY: Albatross Sta. 2229, Lat. 37°38.40″, Long. 73°16.30″W, 2604 m.

TYPE SPECIMEN: Holotype: USNM No. 45752. Examined (JAA).
(Note: 4 specimens from Knorr Sta. 307, 12°34.4′N, 58°59.3′W, 3862 m, BM(NH) No. 1990016).

Nucula trigona Verrill 1885, p. 438; (*non* Bronn, 1849; *non* Seguenza 1877).
Nucula verrilli Dall, 1886, p. 248; 1889, p. 42; 1890, p. 257, pl. 14, Fig. 4; Bush 1893, p. 240, pl. 1, Figs 6, 7; Verrill & Bush, 1898, p. 853, pl. 95, Fig. 10; Clarke, 1962, p. 49; Pequegnat, 1972, p. 74.
Brevinucula verrillii Schenck, 1934, p. 41; James, 1972, p. 24–27, Figs 3, 4; map 1.
Brevinucula verrilli Knudsen, 1970, p. 19, Fig. 3, pl. 1, Figs 6, 7.
Nucula (Brevinucula) verrillii Haas, 1949, p. 7.
Nucula guineensis Thiele, 1931, p. 35; pl. 2, Figs 35, 35a; Clarke, 1962, p. 48, Knudsen, 1970.
Nucula (Brevinucula) guineensis Thiele, 1934, p. 786; Fig. 788.
Brevinucula guineensis Schenck, 1934, p. 4; pl. 5, Figs 22, 2c.
Nucula aequalis Barnard, 1964, p. 3365; Fig. 1c.

DEPTH RANGE: 1976–4749 metres.

The synonymy of this species has been much debated. Thiele, (1931) noted the similarity between *Nucula guineensis* and *B. verrilli*, however, while Schenck, (1934) regarded the two species as congeneric and probably conspecific, Clarke, (1962) recorded them as separate species. Later Knudsen, (1970) recorded them as conspecific and this view was upheld by James, (1972) who compared specimens from the Gulf of Mexico with the type (*N. trigona*, USNM No. 45752, and *Brevinucula guineensis*, Valdivia Sta. 56, ZMHU). Knudsen, (1970) also believes that *Nucula aequalis* (Barnard) is also synonymous with *Brevinucula verrilli*.

MATERIAL

Cruise	Sta	Depth (m)	No	Lat	Long	Gear	Date
			NORTH AMERICA BASIN				
Chain	77	3806	11	38°07.0′N	69°16.0′W	ES	30.06.65
	78	3828	6	38°08.0′N	69°18.7′W	ES	30.06.65
	84	4749	7	36°24.0′N	67°56.0′W	ES	04.07.65
	85	3834	21	37°59.2′N	69°26.2′W	ES	05.07.65
Atlantis II	119	2223	11	32°16.1′N	64°32.6′W	ES	19.08.66
	340	3356	12	38°14.4′N	70°20.3′W	ES	24.11.73
			WEST EUROPEAN BASIN				
Chain	321	2879	5	50°12.3′N	13°35.8′W	ES	29.08.72
	323	3356	3	50°08.3′N	13°53.7′W	ES	21.08.72
	329	4632	29	50°43.3′N	17°44.7′W	AD	23.08.72
			GUYANA BASIN				
Knorr	291	3868	10	10°06.6′N	55°15.4′W	ES	26.02.72
	299	2076	2	07°55.1′N	55°42.0′W	ES	29.02.72
	301	2500	18	08°12.4′N	55°50.2′W	ES	29.02.72
	303	2853	9	08°28.8′N	56°04.5′W	ES	01.02.72
	306	3429	27	09°31.1′N	56°20.6′W	ES	02.03.82
	307	3862	15	12°34.4′N	58°59.3′W	ES	03.03.72
			CANARIES BASIN				
Discovery	6704	2129	23	27°44.9′N	14°25.0′W	ES	17.03.72
	6707	2593	2	27°29.2′N	15°26.5′W	ES	17.03.68
	6709	2351	10	27°29.8′N	15°20.1′W	ES	18.03.68
	6710	2670	6	27°23.6′N	15°39.6′W	ES	19.03.68
	6711	2988	1	27°14.9′N	15°36.3′W	ES	19.03.68
			CAPE VERDE BASIN				
Atlantis II	138	1976	2	10°36.0′N	17°52.0′W	ES	04.12.67
	139	2187	3	10°33.0′N	17°53.0′W	ES	04.12.67
	141	2131	1	10°30.0′N	17°51.5′W	ES	05.02.67
	143	2095	4	10°35.0′N	17°44.0′W	ES	05.02.67
	144	2357	9	10°36.0′N	17°49.0′W	ES	05.02.67
	145	2185	10	10°36.0′N	17°49.0′W	ES	06.02.67
	146	2891	4	10°39.5′N	17°44.5′W	ES	06.02.67
	147	2934	51	10°38.0′N	17°52.0′W	ES	06.02.67
	148	3828	2	10°37.0′N	18°14.0′W	ES	07.02.67
	149	3861	7	10°30.0′N	18°18.0′W	ES	07.02.67
			MID ATLANTIC				
Atlantic II	155	3783	2	00°03.0′S	27°48.0′W	ES	13.02.67
			GUINEA BASIN				
Walda	DS25	2470	56	02°19.8′N	07°49.2′W	SD	00.00.71

SHELL DESCRIPTION

Except that he omits the fact that *B. verrilli* is without a well-defined resilifer, the original description by Verrill, (1885) is detailed and accurate.

Shell deeply triangular, robust, lustrous, equivalve, inequilateral; surface smooth, lustrous sometimes with fine irregular radiating striations; umbo approximately medial, orthogyrate, with faint ridge running from umbo to the postero-lateral angle; when postero-dorsal margin orientated vertically, antero-dorsal margin is below horizontal; lunule lanceolate, faint, escutcheon more distinct; resilifer not well-defined; ligament approximately triangular; hinge plate stout, hinge teeth chevron-shaped, the number varies with size, 4 posterior and 5 anterior teeth in a specimen 2.6 mm in length and 7 posterior and 9 anterior teeth in specimen 4.1 mm in length.

SHELL MEASUREMENTS OF *Brevinucula verrilli*

Dimension (mm)	No	Mean	SD	Max	Min
NORTH AMERICA BASIN					
Length	7	2.31	1.05	3.94	1.06
Width		1.21	0.53	2.08	0.60
Height		2.25	1.11	4.06	0.99
WEST EUROPEAN BASIN					
Length	29	2.35	0.75	3.95	1.00
Width		1.18	0.30	1.83	0.59
Height		2.33	0.77	4.04	0.93
CANARIES BASIN					
Length	7	2.64	1.43	4.55	1.25
Width		1.37	0.68	2.41	0.73
Height		2.59	1.43	4.47	1.20
CAPE VERDE BASIN					
Length	19	4.01	1.02	5.19	1.63
Width		2.02	0.53	2.87	0.97
Height		3.99	1.03	5.09	1.59

INTERNAL MORPHOLOGY

The posterior adductor muscles are more-or-less oval with the anterior muscle the more elongate and convex posteriorly. The 'quick' and 'catch' portions are approximately equal. The gill axis lies parallel to the postero-dorsal margin of the shell. The gill plates number 16 in a specimen 3.9 mm in length. The palps are moderately large and, in the same specimen, the palp ridges number 27. The 'byssal' gland is large. The stomach is relatively small and the hind gut is extensive (Fig. 31). Note the course of the gut is complex even to the extent that a few loops are to the left of the stomach. The species has large characteristic loosely arranged gonads. The maximum recorded egg diameter is 125 µm and development is likely to be lecithrotrophic. There are 260 eggs in a specimen 4.3 mm total length (Scheltema, 1972).

The species was originally described as having a triangular 'chondrophore' and, as Vokes, (1949) points out, although this is unique among Recent nuculids, it occurs in the Palaeozoic species *Nuculoidea opima* Hall and *Nuculopsis girtyi* Schenck. More-recent studies show that although the hinge plate is broad *B. verrilli* is without a chondrophore but has a well-developed resilifer (Allen & Hannah, 1986). This may also be the case in the Palaeozoic species. According to Moore, (1969) *B. verrilli* is not present in the fossil record prior to the Miocene.

DISTRIBUTION

B. verrilli is restricted to the deep sea and no comparable shallow-water counterpart exists.

Verrill, (1885) collected the species from the North America Basin at U.S. Fisheries Commission Stations 2194, 2228 and 2229 at depths ranging from 2086–4077 m. Dall, (1890) reported specimens from Station 2754, east of Tobago and Station 2760, north from Ceara, Brazil in 1610 and 1865 metres respectively and summarized the then known geo-
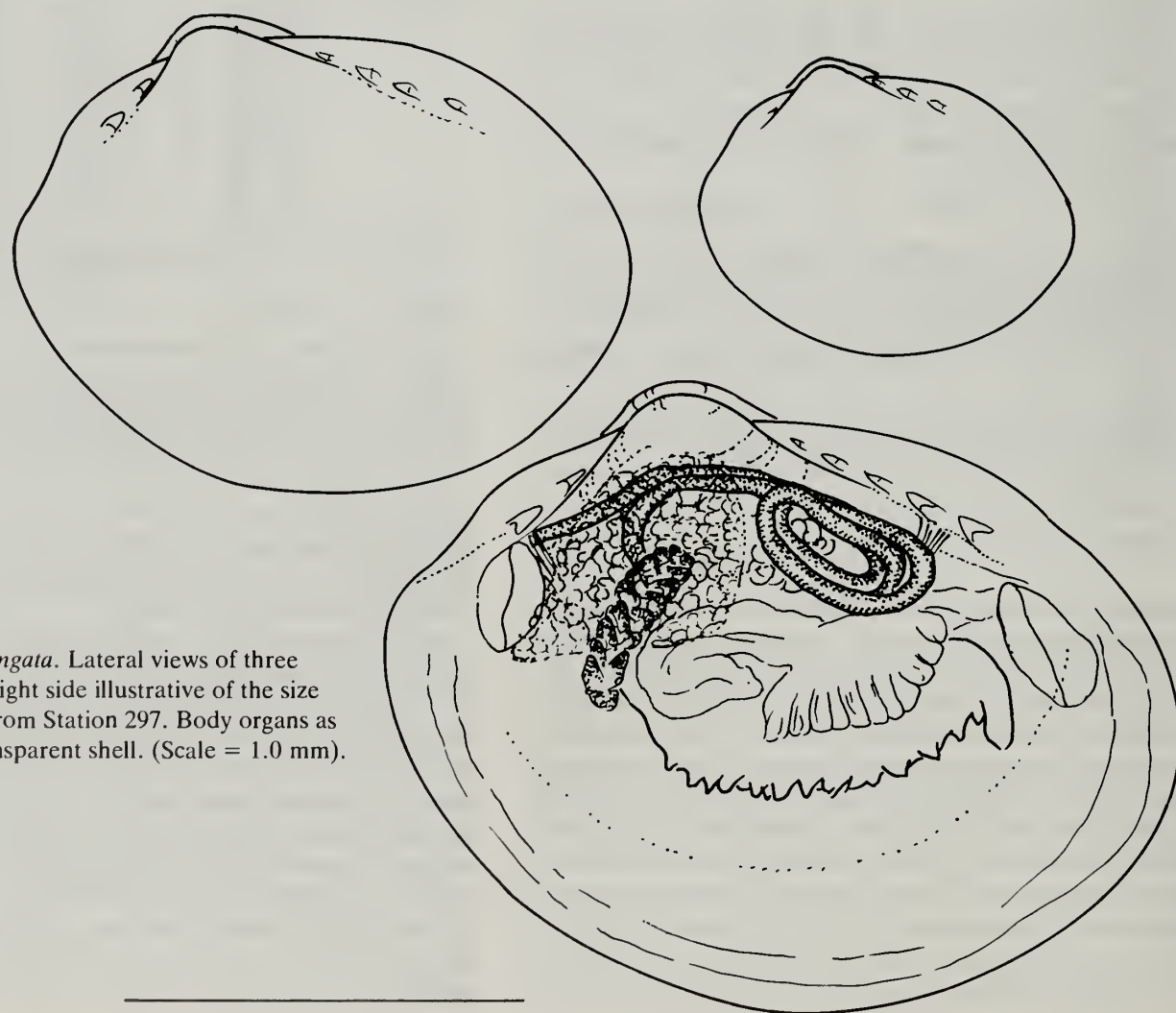

Fig. 27 *Nuculoma elongata*. Lateral views of three specimens from the right side illustrative of the size range of specimens from Station 297. Body organs as seen through the transparent shell. (Scale = 1.0 mm).

graphical distribution as from latitude 39°44', south to Yucatan at depths from 538 to 3340 metres (Dall, 1927). Thiele, (1931) described *N. guineensis* from the Guinea Basin ('Valdivia' Stations 56, 63 and 71) and Knudsen, (1970) set the latitudinal limits from 40°N to 12°S in the western Atlantic and from 4°N to 6°S in the eastern Atlantic. Pequegnat, (1972) reported the species from the gulf of Mexico and this was confirmed by James, (1972) who collected from 12 Stations in depths from 914 to 3475 metres.

The report (Knudsen, 1970) that the species occurs at 12°S in the western Atlantic is not confirmed. Specimens taken from this latitude differ from *Brevinucula verrilli*. Little material was taken from the Brazil Basin and the absence of *B. verrilli* may be related to insufficient sampling.

B. verrilli is predominantly a North Atlantic species. Its distribution in the temperate eastern Atlantic is now extended to 50°N. Despite intensive sampling it is not recorded from the Rockall Trough and Bay of Biscay and the reason for this is not immediately apparent. It has a vertical range that extends into depths shallower than both these regions. No comparable species occurs in the angola and the Argentine Basins, however, Barnard, (1962), described *Nucula aequalis* from off Cape Point, South Africa and this may be synonymous with *B. verrilli* (Knudsen, 1970). If this is correct it could be that this is a case of a species with bipolar distribution Ekman, (1953). This phenomenon is unusual among deep sea bivalves and would be the first reported case of an abyssal bivalve to have such a distribution.

B. verrilli occurs at greater depths than any other member of the Nuculidae and its distribution extends on to the abyssal plain.

Brevinucula subtriangularis (new species)

Figs 33–34

TYPE LOCALITY: Atlantis II Sta. 167, Lat. 7°58'S Long. 34°17'W.

TYPE SPECIMEN: Holotype: BM(NH) No. 1990009; paratypes at present lodged at Woods Hole Oceanographic Institution (5 specimens in lot).
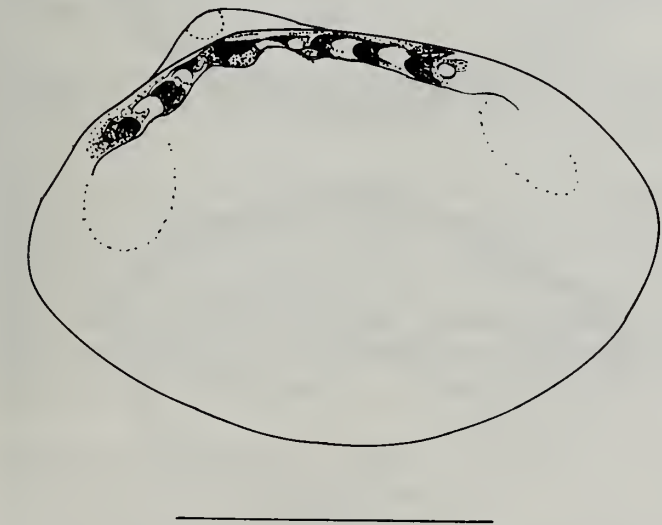
DEPTH RANGE: 943–1007 metres.

Fig. 28 *Nuculoma elongata*. Internal view of left valve of shell form Station 297. (Scale = 1.0 mm).
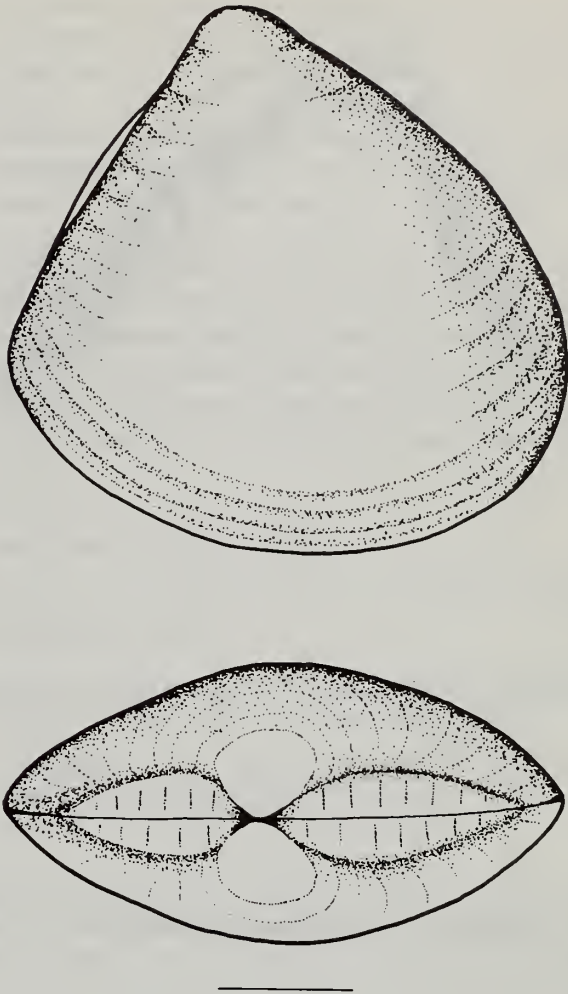

Fig. 29 *Brevinucula verrilli*. Lateral and dorsal view of a shell from Station 85. (Scale = 1.0 mm).

MATERIAL

Cruise	Sta	Depth (m)	No	Lat	Long	Gear	Date
			BRAZIL BASIN				
Atlantis II	167	943–1007	31	07°58.0'S	34°17.0'W	ES	20.02.67

SHELL DESCRIPTION

Shell small, robust, lustrous, very smooth, equivalve, inequilateral; umbo posterior to midline, opisothygrate; when posterior margin orientated vertically, antero-dorsal margin is horizontal; lunule indistinct, escutcheon marked by faint ridge from umbo to the postero-ventral angle; resilifer large; ligament approximately triangular; hinge plate stout, hinge teeth chevron-shaped, 5 posterior and 9 anterior teeth in a specimen 4.9 mm in length.

SHELL MEASUREMENTS OF *Brevinucula subtriangularis*

Dimension (mm)	No	Mean	SD	Max	Min
		BRAZIL BASIN			
Length	2	4.95	0.06	5.00	4.91
Width		2.98	0.44	3.29	2.67
Height		4.58	0.15	4.69	4.48
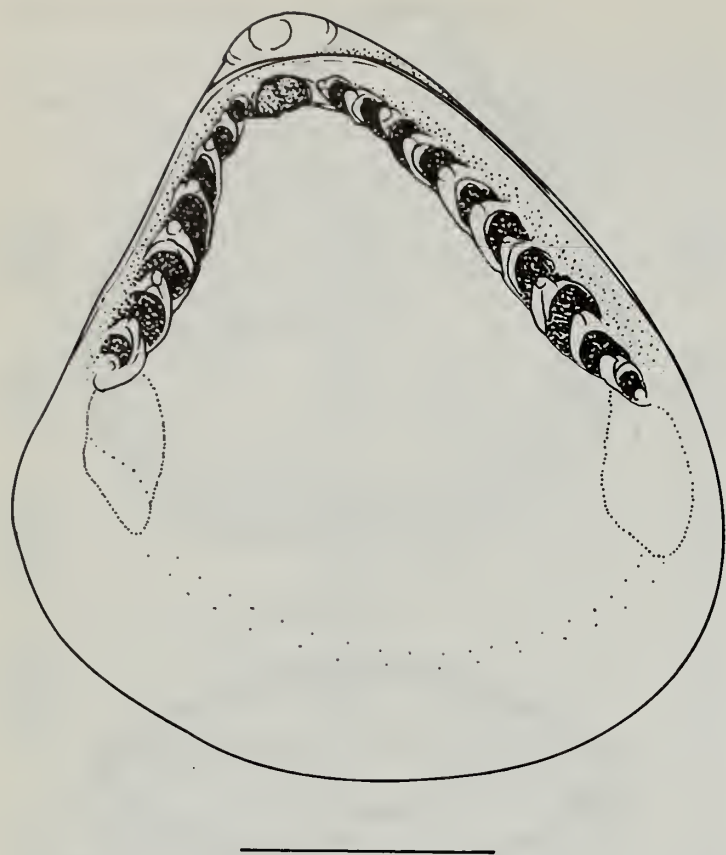
Fig. 30 *Brevinucula verrilli*. Internal view of left valve of shell from Station 85.
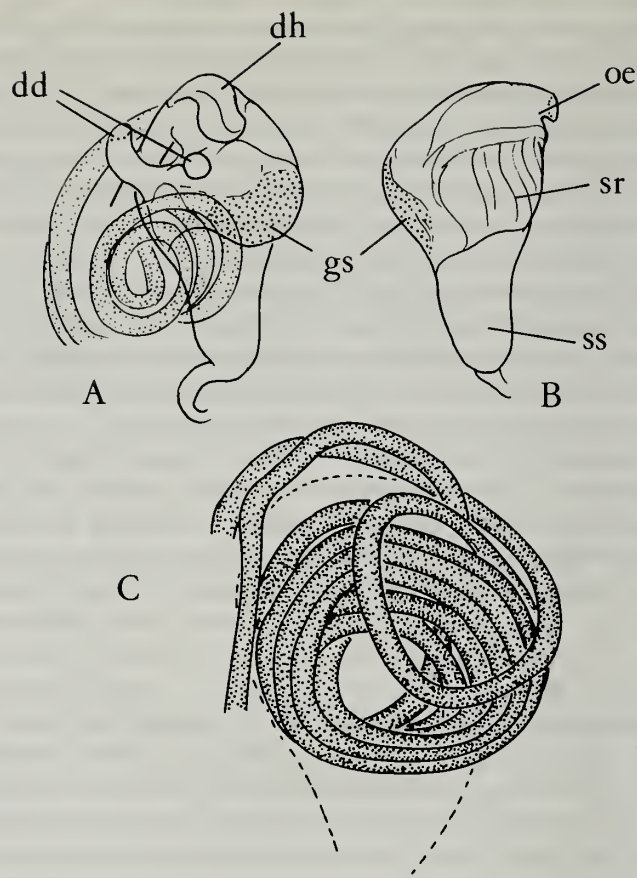

Fig. 32 *Brevinucula verrilli*. A. Lateral view of left side of stomach, and coils of hind gut on the left side of stomach; B. Lateral view of the right side of stomach to show posterior sorting area; C. The coils of the hind gut to the right side of the stomach, the stomach outlined by dashed lines. (For key to abbreviations see p.63).

INTERNAL MORPHOLOGY

The adductor muscles are more or less oval. The anterior muscle is larger than the posterior and both have a shape similar to those of *B. verrilli*. The 'quick' and 'catch' portions are approximately equal in size. The gill axis is parallel to the posterior margin of the shell with 15 gill plates in a specimen

Fig. 31 *Brevinucula verrilli*. Semidiagrammatic view of right side of body to show arrangement of organs. (Scale = 1.0 mm; see Fig. 19 for identification of parts).

Fig. 33 *Brevinucula subtriangularis*. Lateral and dorsal view of a shell from Station 167. (Scale = 1.0 mm).

5 mm in length. The palps are moderately large and there are 28 palp ridges in the same specimen. The foot is similar in proportion and orientation to that of *B. verrilli*. The 'byssal' gland is large. The stomach is relatively small and the hind gut is extensive. The gonads are large and loosely arranged.

Although this species differs in shape from *B. verrilli* eg. The shells are slightly longer than high, they have features in common. They have a very large resilifer, and have a non-crenulate inner ventral shell margin. Both species have rounded anterior and posterior shell margins. *B. subtriangularis* is slightly heteromyarian, and the shape of the anterior adductor muscle is similar to that of *B. verrilli*. Both species have a comparatively small stomach, and large, loosely arranged gonads.

DISTRIBUTIONS

Brevinucula subtriangularis was collected from one Station at mid-slope depth from the Brazil Basin. No comparable species are present in the Holocene formations of Guyana (Altena, 1968), even though species of *Brevinucula* appear to have been common in Jurassic and Triassic shallow seas.
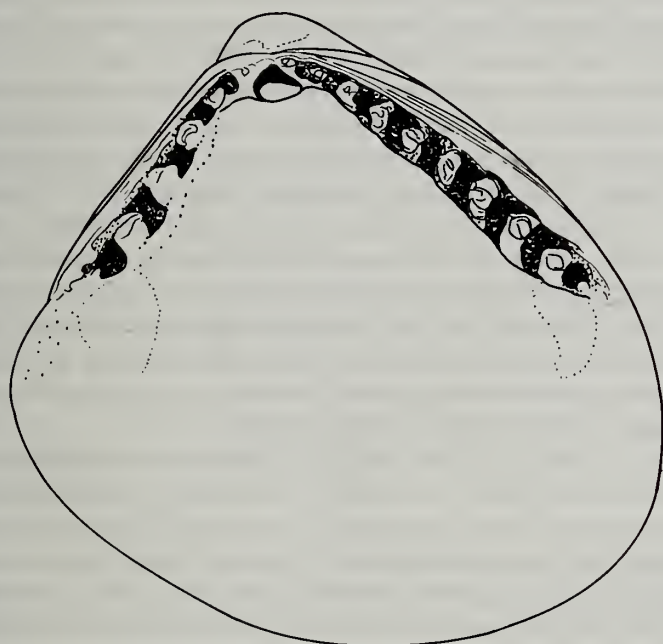

Fig. 34 *Brevinucula subtriangularis*. Internal view of left valve of shell from Station 167. (Scale = 1.0 mm).

OTHER ATLANTIC DEEP-SEA NUCULIDS

Here we list species not discussed so far in the text that have been described as having a deep-sea distribution. This latter we construe as having a population 'peak' below 500 metres, clearly below the shelf-slope break. We have excluded species from the Norwegian Basin in that its abyssal bivalve fauna is almost without exception self-contained (Bouchet & Warén, 1979).

Nucula crenulata Adams, 1856

TYPE LOCALITY: Guadaloupe.

TYPE SPECIMEN: Probable syntype, BM(NH) 1991012 (examined PR).

Nucula crenulata Adams, 1856; Dall, 1886, p. 247, pl. 7, Fig. 2 (in part); 1889b, p. 42, pl. 8, Fig. 2.
Nucula crenulata var obliterata Dall, 1881, p. 123; Clarke, 1962, p. 48.
Nucula culebrensis obliterata Johnson, 1934, p. 16.
Nucula obliterata James 1972, p. 39–40, Figs 19, 20, Map 2; (*non Nucula obliterata* Knudsen, 1970).

Dall, (1881, 1886, 1890) reported this species from the Florida Straits, the south east of the Gulf of Mexico, the southeastern Caribbean, and off Cape Hatteras from depths of 168 to 1472 metres James, (1972) also recorded the species from the Gulf of Mexico from depths of 969 to 1280 metres.

N. crenulata resembles the Tertiary species *Nucula striatissima* Seguenza.

Nucula culebrensis Smith, 1885

TYPE LOCALITY: 'Challenger' Sta. 14, Lat. 18°38′30″N, Long. 65°05′30″W, 714 m.

TYPE SPECIMEN: Holotype not designated; syntypes (5 valves, BM(NH) 1887.2.9.2912–3) (examined PR).

Nucula culebrensis Smith, 1885, p. 228, pl.18, fig. 11, 11a; James, 1972, p. 36–38, Figs 15, 16, Map 2.

REMARKS

The original description by Smith, (1885) is detailed. The species is similar in shape to *Deminucula cancellata* but differs in having tubercles that surround the lunule. The species originally taken off the West Indies is also recorded in the Gulf of Mexico 417–1518 metres (James, 1972), however, these latter shells were badly eroded and were thought to have been vertically displaced.

Deminucula fernandinae (Dall, 1927)

TYPE LOCALITY: 'Albatross' Sta. 2668, Lat. 30°58′N, Long. 79°38′W, 678 m.

TYPE SPECIMEN: Holotype not designated, but syntypes (two pairs conjoined valves and one valve) exist: USNM No. 108198 (examined JAA).

Nucula fernandinae Dall, 1927, p. 8; Johnson, 1934, p. 16.

Dall, (1927) gives only a brief description but compares *D. fernandinae* with *N. culebrensis* and *N. crenulata var obliterata*.

This species was described from two whole specimens and one larger valve (Dall, 1927). A single left valve of this species is also recorded by James, (1972) from the Gulf of Mexico in 2528 metres but is probably vertically displaced. This species is similar to *D. atacellana* and like this species has a prominent concentric sculpture and is without a well-defined resilifer.

Nucula zophos Clarke, 1960

TYPE LOCALITY: 'Alpha' Sta. 6, Lat. 84°28′N, Long. 148°28′W, 1691 m.

TYPE SPECIMEN: Holotype: Mus. Comp. Zool. Harv. No. 222067 (examined JAA).

Nucula zophos Clarke, 1960, p. 5; pl. 1, Figs 15–18, 1963,

p. 99; Paul & Manzies 1973, p. 127; Bernard, 1979, p. 11, Fig. 2; Knudsen, 1985, p. 98.

The original description by Clarke, (1960) is detailed. The species was found by Clarke, (1960) about 800 miles north of Port Barrow, Alaska, in depth ranges from 1464–1660 metres. Bernard, (1979) has also collected the species from 2377 m in the Beaufort Sea. Bernard, (1979) states that the species is widely distributed in the archibenthal of the Laurentian Basin. Knudsen, (1985) records the species off northeast Greenland and from 530–2237 metres—a much greater range than found by Bernard, (1979). The species appears to be restricted to the Polar and Laurentian Basins and has not been reported south of the Iceland-Faeroe ridge nor, surprisingly in the Norwegian abyssal basin (Bouchet & Warén, 1979). It bears a close resemblance to *N. callicredemna*.

Pronucula benguelana Clarke, 1961

TYPE LOCALITY: R/V Vema Sta. 14, Lat. 30°14.9'S, Long. 13°03'E, 3116 m.

TYPE SPECIMEN: Holotype: Mus. Comp. Zool. Harv. No. 224964 (examined JAA).

Pronuncula benguelana Clarke, 1961, p. 368–369, pl. 3, Figs 9, 11.
Nucula (Pronucula) benguelana Barnard, 1962, p. 446; Fig. 11a.

The original description by Clarke, (1961) is detailed, but although Clarke, (1961) described this species as having a non-crenulate ventral margin, *Pronucula benguelana* has radial sculpturing which is typical of species with marginal crenulations and we confirm Barnard, (1962) who describes the species as having a crenulate margin. Note: Barnard regards *Pronucula* as a subgenus of *Nucula*.

This species, which is not present in any of the Atlantic abyssal material reported on in this study, appears to be restricted to the Cape Basin (Clarke, 1961). It has been described by Barnard, (1962) as occurring west of Cape Point, South Africa and, according to Clarke, (1961) it is a member of a deep-sea species complex present in the southern Indian and Pacific Oceans.

Finally brief mention should be made of *Nuculoma corbuloides* (Seguenza, 1877) and *Nucula striatissima* (Seguenza, 1877). Both species were described from Tertiary fossils. Thereafter Recent specimens from the Mediterranean and the Eastern Atlantic are listed in Jeffreys, 1879, Locard, 1898, and Massey, 1930. These specimens are relatively few in number and taken from slope depths. Despite extensive sampling by French workers in the Bay of Biscay these species have not been recorded in recent years.

ORIGIN, ANTIQUITY & DIVERSITY OF THE DEEP-SEA NUCULIDS

The abyss has been regarded as a sanctuary for an archaic relict fauna (Ekman, 1953; Dahl, 1954; Zenkevitch & Birstein, 1956, 1960; Birstein, 1959, 1969; Zenkevitch, 1969) and there are many claims that 'living fossil' representatives of groups occur eg. Radiolaria (Haecker, 1908), Hexactinell-

ida (Ijima, 1927), Crinoidea (Clark, 1915), Asteroidae (Zenkevitch & Birstein, 1956), Holothurioidea (Theel, 1882), Harpacticoida (Zenkevitch & Birstein, 1956), Mysidacea (Tattersall, 1921), Isopoda (Wolff, 1956a), Tanaidacea (Wolff, 1956b), Decapoda (Doflein, 1904; Balss, 1925, 1955), Pisces (Andraishev, 1953) and Mollusca (Locard, 1898; Bonnevie, 1912; Zenkevitch & Birstein, 1960; Parker, 1962; Filatova, 1959; Filatova *et al.*, 1968). The majority of deep sea bivalves belong to groups whose geological record dates back to the Ordovician (Allen, 1978).

The dominant bivalve group of the deep sea, the Protobranchia, is present in the earliest assemblages of the fossil record and protobranch genera such as *Tindaria, Malletia, Neilonella, Neilo, Nuculana, Yoldia, Yoldiella* and *Nucula* are regarded by Zenkevitch & Birstein, (1960) as ancient elements of the deep-sea fauna. In contrast relatively few protobranch species occur in shelf seas and these are almost entirely restricted to the families Nuculidae and Nuculanidae (Allen, 1978).

Of the divisions of the Nuculidae as defined by Schenck, (1939) (p. 64) two occur in the deep Atlantic namely those with crenulate shell margins and those with smooth shell margins. Species with divaricate shell sculpture do not occur (nor do they occur in shallow waters of the Atlantic).

Species with smooth margins are found throughout geologic time. One of the earliest from the Pennsylvanian of Iowa, *Nuculopsis ventricosa* (Hall) has a shell morphology that differs little from Recent species (Schenck, 1939). Species of *Nuculoidea* date from the Silurian and Devonian (McAlester, 1962; Soot-Ryen, 1964). *Nuculoma* dates from the Jurassic (Cossmann & Thiery, 1907). In contrast crenulate species have a far less protracted geologic history and extend no further back than the Cretaceous (a possible exception is the Mississippean Carboniferous species *Nucula schumardiana* (Cox, 1940; Vokes, 1949).

Vokes, (1949) also reported the Palaeozoic species '*Nuculoidea opima* Hall' as having microscopic crenulations. Because this did not fit into the Schenck, (1939) classification Vokes, (1949) suggested that such species should be placed in a separate group from the crenulate and non-crenulate forms. This includes the species of *Brevinucula*. Moore, (1969) states that *Brevinucula* does not appear in the geological record prior to the Miocene.

Thus, the present study supports the concept of antiquity. Species with non-crenulate inner ventral shell margins are descended from a more-archaic group than species with a crenulate inner ventral margin and the former, which have representatives in the Ordovician, are far the more abundant in the deep sea. In contrast, the crenulate species which did not appear in the fossil record until the Cretaceous are more abundant in shallow water. Of 12 shallow-water nuculids of the North Atlantic, 4 have non-crenulate shell margins, whereas of 8 deep-sea Atlantic species (not including *Brevinucula*) 6 have non-crenulate margins. As Knudsen, (1970) suggests, there probably has been a descent of shallow-water species into the abyssal zone throughout geological history. Therefore it would be expected that along with species of deep-water origin there exist deep-water species closely related to shallow-water species. Zenkevitch & Birstein, (1960) suggest that it is possible to distinguish between ancient and secondary deep-water species by their patterns of distribution. In the case of the secondary species, their diversity decreases with increasing depth whereas the ancient groups tend to show increasing diversity with increasing

depth which diminishes only when encroaching lower abyssal depths or the perturbed trenches and vent systems. The distribution pattern of deep-sea 'non-crenulate' nuculids would suggest that they are an ancient rather than a secondary deep-water group.

It has been assumed that one of the more important factors restricting downward migration is temperature and that polar coastal regions yield species of the necessary eurybathic capacity to invade the deep sea (Bruun, 1956; Kussakin, 1973). The close affinity between the Arctic shallow-water species, *N. bellotii* and *Nuculoma similis* and the Greenland species *N. corticata* with *N. granulosa* would appear to support this conclusion.

Kussakin, (1973) noted that primitive isopods are principally confined to tropical waters, whereas isopods of cold and temperate regions and especially the deep-sea are considered phylogenetically recent. He speculated that tropical faunas gave rise to temperate faunas which then gave rise to cold-water faunas and that from the cold-water faunas of the Antarctic shelf came the initial and main source of deep-sea faunas. The adaptation of the shelf fauna to deep-sea conditions was thought to have been promoted by climatic cooling and subsequent glaciation which occurred in the Miocene and approximately a million years earlier than in the northern hemisphere, and therefore Antarctica became the sole zone supplying cold oxygen bearing water into the abyssal zone. The thickening ice was thought to cause the gradual isostatic dipping of the continent and shelf by as much as 900 m and so the Antarctic shelf-fauna was slowly forced deeper. The movement of cold Antarctic water into the abyss and then northwards would have then facilitated subsequent distribution. In contrast to Kussakin, (1973), Hessler *et al.*, (1979) also on the basis of biogeographical studies of deep-sea isopods, argue that the presence of species closely related to deep-sea species in shallow high latitudes is the result of subsequent emergence and that many deep-sea species evolved *in situ*.

Curiously, although evidence suggests that a few deep-sea nuculids had their origin in the Arctic region, there is no indication that a similar process occurred in the Antarctic. There is a dearth of nuculids in the deep Antarctic (Dell, 1972) and to date only *N. notobenthalis* Thiele, has been described and this does not appear to be similar to any other deep-sea Atlantic species. It is perfectly feasible that 'non-crenulate' nuculids, which are more diverse in the deep sea, may have given rise to shallow water species such as *Nuculoma tenuis* and *N. bellotii*. Some abyssal genera are cosmopolitan and thus they are potentially available for emergence into any suitable shallow-water environment (Hessler *et al.*, 1979). This would explain the ubiquity of *N. tenuis*.

There are two strict shallow-water nuculids in the Arctic (Clarke, 1960; Bernard, 1979), 7 or 8 species occur in the temperate zone (5 on the east coast of the North Atlantic (Allen, 1954), and 3 or 4 on the west coast (Mighels & Adams, 1842; Hampson, 1971; Abbott, 1974). Six species occur in the western tropical region between the Caribbean and Surinam (Dautzenberg, 1900; Weisbord, 1964; Altena, 1968; Moore, 1977). There does not appear to be any certain information relating to the number of species present in the eastern tropical Atlantic, but there is likely to be a further assemblage of species. On this basis nuculid diversity would appear to increase slightly towards the tropics. Prior to the radiation of the other major shallow water bivalve deposit-feeding group the Tellinacea, in the middle Cretaceous nuculid diversity in the tropics was probably far greater and, since the 'crenulate' nuculid species did not evolve until the Cretaceous, the assemblages would presumably have been mainly composed of 'non-crenulate' forms. Tellinaceans are not present in the abyss and only two species are present at lower slope depths (Allen & Sanders, 1966), but massive radiation of tellinaceans may have resulted in the extinction of the shallow water tropical nuculid predecessors and may eventually lead to the loss of others in higher latitudes and the deep-sea. This totally ignores physiological aspects which presently constrain the colonization of the deep-sea by tellinaceans and favour the nuculacean presence there (Allen, 1978).

Sanders & Hessler, (1969) found that in general, diversity in abyssal basins was of a similar order of magnitude to that found in some shallow tropical seas and well exceeds that in cold temperate shelf seas. Unlike the nuculanids the vertical diversity of the nuculids does not conform to this generalization. Although, there is an increase in the diversity of 'non-crenulate' species with depth, overall nuculid diversity decreases. For example, on the temperate North East Atlantic shelf (<200 m) there are 5 species (Allen, 1954), whereas in the West European Basin (>1500 m) there are only 3 species. In the western tropics around Guyana the disparity is 7 shelf-species (Altena, 1968; Moore, 1977) and 4 abyssal species. In the temperate western Atlantic there are 4–5 shelf species (Mighels & Adams, 1842; Hampson, 1971; Abbott, 1974) as compared with 5 abyssal species in the North America Basin. The reduction in nuculid diversity with increasing depth in the north east and tropical west Atlantic may be related to the fact that 'crenulate' species were not present in shallow water before the Cretaceous and therefore only comparatively recently have they invaded the deep sea.

DISCUSSION

The species described here are based on morphological characters and therefore would be regarded by numerical taxonomists as morpho-species rather than biological species as defined by Mayr, (1949). There is no biological reason why inability to interbreed should always be traceable to morphological differences (Savory, 1962), and classifications based on similarity alone may not always reflect genetic affinity. Nevertheless, the morphological differences between intrabasin species are sufficiently large to more-or-less exclude the possibility that they are variants of a single species. Widely distributed species such as *D. atacellana* with numerous populations as far apart as the Rockall Trough and the Argentine Basin (approximately 7000 miles) may turn out to be more than one species on the basis of, say, electrophoretic evidence. Overall the deep-sea bed is not subject to large amounts of environmental heterogeneity, consequently it is hypothesized that populations in this environment would maintain little genetic variability (Manwell & Baker, 1970; Grassle, 1972; Grassle & Sanders, 1973). In fact deep-sea species are far from genetically depauperate and may maintain levels of genetic variability which are average or above average for marine invertebrates (Gooch & Schopf, 1972; Ayala & Valentine, 1974; Valentine & Ayala, 1975; Ayala *et al.*, 1975; Murphy *et al.*, 1976), and have as much if not more potential for change as organisms from other environments.

Although the nuculids are preadapted for deep-sea existence (eg. feeding and shell composition) their life in deep water has been accompanied with adaptation. This includes reduction in the area of the gill and number of plates, the elongation of the hindgut, a reduction in the number of ciliated grooves in the stomach, an increase in egg size and a reduction of body size and low productivity. Probably all are adaptations to nutritional impoverishment but are also likely to be accompanied by physiological adaptation to low temperature and high pressure. Nevertheless, none of the Atlantic deep-sea nuculids can be regarded as truly abyssal since no species reaches an *optimal* population density at abyssal depths (ie. >4000 m). Only two species, *B. verrilli* and *D. atacellana*, have distributions which exceed 4000 m and both of these are also found at slope depths. Indeed, most species are restricted to the continental slope with diversity reaching a maximum between 1000–2000 m. Reduction in diversity as abyssal depths are approached is recorded in a number of macrofaunal groups (Sanders *et al.*, 1965; Rex, 1973, 1976) and may be a result of extremely low productivity at these depths. One adaptation to low productivity is the reduction of body size, but there must be a limit to this particular adaptation. Rex, (1973) suggests that productivity affects macrofaunal diversity only when the lower limit of adaptation in size is approached.

Co-existing protobranchs having closely similar feeding habits and apparently identical food in their guts has to be explained against the apparent lack of potential niches within the soft monotonous abyssal sediment. Originally 'niche' was defined as the subdivision of the environment within which the species lives (Grinnell, 1917). Hutchinson, (1957) reformulated the concept in terms of set theory such that if each environmental variable is given a co-ordinate in an N-dimensional space, then a niche can be defined as a multi-dimensional hypervolume in which the fitness of the individual is positive. Real separation of species may be based mainly on trophic rather than physical or chemical factors (Green, 1971), and this may well apply in the deep-sea where if protobranch niche demarcation does exist in the deep-sea environment, it appears to be very subtle, and may be a product of biochemical specialization and differing spatial requirements (Grassle & Sanders, 1973; Allen, 1983).

The distribution of cosmopolitan species such as *Deminucula atacellana* and *Nuculoidea subovata* seems to be attributable to the production of pelagic larvae. Species which have direct development, such as *Nuculoma similis* and *Nucula delphinodonta* have restricted distributions. Pelagic larvae of deep-sea protobranchs have never been collected from surface waters, therefore, transportation must take place in deep water. The velocity of deep-sea currents range from 1.5 to 44 cm/sec (Knauss, 1965; Webster, 1969; Schmitz *et al.*, 1970; Hogg, 1983; Saunders, 1983), and if the duration of larval transport is only a few days, larvae could in theory be transported many kilometres.

Pelagic larvae are not only important as a means of dispersal but also for maintaining genetic continuity. The lack of morphological differences between widely separated populations of *D. atacellana* and *N. subovata* suggest frequent genetic exchange between these populations and that long-lived larvae exist in the deep sea. Discontinuities in the distribution of deep-sea nuculids are difficult to explain but could be related to a dispersal controlled by prevailing currents and ridge systems.

The results of this study and that of Bouchet and Warén, (1979) show that none of the North Atlantic abyssal nuculid species occur north of the North Atlantic Transversal Ridge. Although both *D. atacellana* and *N. subovata* are common in the Rockall Trough, adjacent to the ridge, neither are found in depths less than 1000 m and it must be that their larvae are unable to travel north into the Norwegian Basin against the prevailing deep cold water currents originating in high latitudes (Lynn & Reid, 1968). There also appear to be no nuculids common to the abyss of both the Atlantic and the Antarctic (Soot-Ryen, 1951; Powell, 1960, 1965; Dell, 1964, 1972) even though there appears to be no barrier. The Cape Basin also appears to have few affinities with the rest of the Atlantic as far as nuculids are concerned. There are no species common to the Cape Basin and the adjacent Angola Basin, yet two species found in the Angola Basin are found in other Basins on both sides of the equator. Clarke, (1960) only found one nuculid species, *Pronucula benguelana*, in the Cape Basin, and neither this species nor the genus is found in any other Atlantic Basin.

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